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# CATALOGUE OF THE PONTIAN BOVIDAE OF EUROPE 

IN THE DEPARTMENT OF GEOLOGY

By
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LONDON:
PRINTED BY ORDER OF THE TRUSTEES OF THE BRITISH MUSEUM
SOLD AT
The British Museum (Natural History), Cromwell Road, S.W. 7
AND BY
B. Quaritch, Ltd.; Dulau \& Co., Ltd.; The Oxford University Press; and

Wheldon \& Wesley, Ltd., London; also by Oliver \& Boyd, Edinburgh
1928


Drinted in Great Jbritain
WILLIAM CLOWES \& SONS, LIMITED,
London and Beccles.

## PREFACE

On assuming the Keepership in I924 I found the Geological Department deprived of both the distinguished authorities on extinct vertebrata who had been on the staff. Fortunately, Dr. G. E. Pilgrim of the Geological Survey of India, whose competence in such matters is well known, was coming home on long leave, and he very kindly arranged to join us as temporary Assistant. When the task for which he had been specially engaged was completed, it was thought that the remainder of his leave might be usefully employed in an attack on our large collections of Mammalia from those Upper Miocene or Lower Pliocene deposits of Central and Southern Europe to which the name Pontian has been given. A start was therefore made with the Cavicornia or Bovidae, which is represented in Europe mainly by that group to which the English name Antelopes is fairly applicable.

Dr. Pilgrim had barely completed his work before he was obliged to return to India, leaving his manuscript with me for such editorial revision as might be needed to bring it into conformity with the rules adopted in the Department for similar publications. Hardly had he gone before we received the monograph on a similar collection by Dr. J. Andree, to which reference is made in the Introduction. Although a copy was immediately sent after Dr. Pilgrim, it was impossible for him to deal adequately with all the questions raised by this prior publication. There were other matters on which, as it seemed to me, more might have been said by Dr. Pilgrim had he not been pressed for time.

A visit to Hungary last summer brought me into touch with still further material -notably that from the well-known deposit Baltavár-which it appeared needful to include in the Catalogue although hitherto entirely unrepresented in the National Collection. May I here express hearty thanks to many Hungarian friends in Budapest, Baltavár, and Szombathely for their kindness and courtesy?

Seeing the difficulty of discussing all the new points with Dr. Pilgrim, I placed the manuscript in the hands of Mr. A. T. Hopwood with full instructions as to the method of casting. The rearrangements and additions made in consequence have been so extensive that it seemed only fair, to Dr. Pilgrim no less than to Mr. Hopwood, to add the latter's name to the title-page. Although as little change as possible has been made in Dr. Pilgrim's descriptions and conclusions, it is not feasible to distinguish in the text between the work of the two authors; nor does this matter, since, on Dr. Pilgrim's return to England, they have found themselves in complete accord. To both of them my thanks are due.

May this be but the first of a long series of memoirs on our rich collection of Pontian Mammals!

F. A. BATHER.

Department of Geology, British Museum (Natural History), 15th February, 1928.

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# PONTIAN BOVIDAE OF EUROPE 

## INTRODUCTION

This work is based essentially on the collections preserved in the Geological Department of the British Museum, but an attempt has been made to check it, and in some respects to supplement it, by comparison with the foreign collections mentioned below.

Thanks are due to Professor M. Lugeon, of Lausanne, for affording Dr. Pilgrim the opportunity of studying the collections in his charge. We have also to acknowledge the kindness of Professor Marcellin Boule in granting Dr. Pilgrim every facility in Paris for studying Gaudry's Pikermi types, as well as the De Morgan Collection from Maragha which has been described recently by Mr. de Mecquenem. The latter gentleman was good enough personally to show him any specimens of interest, and to point out their individual peculiarities. Finally, we are extremely indebted to Professors Max Schlosser and Ernst Stromer, not only for sending us additional information and measurements of individual specimens, but also for freely placing at Dr. Pilgrim's disposal for purposes of study the entire Samos collection in Munich.
i. Collections in the British Museum.--Of these four are of especial importance because of their size, and because of the number of exceptionally well-preserved specimens they contain. These collections are :
(a) The Bravard Collection, purchased by the Trustees in 1852, containing material from Cucuron, near Apt (Vaucluse), France.
(b) The Major Collection, purchased by the Trustees in 1889 and 1890, containing material collected by Dr. Charles Immanuel Forsyth Major in the neighbourhood of Mytilene in the Isle of Samos.
(c) The Woodward Collection, presented by Mr. Alex. Skouzès, G.C.V.O., in IgoI, contains the specimens collected by Dr. (now Sir) A. Smith Woodward, F.R.S., at Pikermi, Attica, Greece.
(d) The Woodward Collection from Concud, presented by Dr. A. Smith Woodward in 1902, contains material collected by the donor at Concud, Teruel, Spain,

Material derived from other sources, whether by gift or by purchase, is noticed in the lists of specimens.

Few of these specimens have been described, although there are many of them which throw light on previously known species.

The British Museum also possesses specimens from a few extra-European localities, notably from Maragha in Persia and from the Dhok Pathan horizon of India. Those from the former place have been of especial value and interest for purposes of comparison. Where we have had occasion to refer to them we have always mentioned their register numbers, and in one case a skull, of Protoryx longiceps, has been figured.
ii. Collections in Foreign Museums.-A catalogue of another collection made in Samos by Major, and preserved in the Museum at Lausanne, was published in 1894. It contains a few very brief descriptions, reprinted from other papers published in 1891 and 1892, but no figures. In the case of the Antelopes many of the species are still nomina nuda. This list is again referred to below (p. 59).

Further material from Samos, in the Munich Museum, was described by Prof. Max Schlosser in 1904. He worked without regard to Major's collections in London and Lausanne, and, in some cases, gave new names to species which Major had already named. In these cases Schlosser's names have the priority, and the Munich specimens stand as the types of the species.

Additional collections of fossil antelopes from Samos contained in the Geological Institute of Münster, in the State Museum of Natural History at Vienna, and in the Natural History Museum at Stuttgart, have been described recently (September, 1926) by Dr. J. Andree. New species and genera occur in Andree's work, but, so far as we are aware, these cannot be identified with any of those for which Major had already proposed valid names. Unfortunately this monograph appeared only after Dr. Pilgrim had returned to India. It was not possible for Mr. Hopwood to examine the collections therein dealt with, and, owing to this, our comments on the monograph are necessarily brief. In most cases a free translation of the more important of Dr. Andree's remarks is all that has been attempted.
iii. Classification.-The Antelopes are placed in a family which includes the Oxen, Sheep, and Goats. For this family Schlosser uses the name Cavicornia, whereas the general usage is to keep the older name Bovidae. All members of this family are characterized by the possession of hollow horns, sheathing a bony core. It is impossible to maintain a more rigid distinction between the true oxen and the antelopes than between the several groups of antelopes themselves. A careful study of the fauna of the Pontian of India has shown that there is a gradual transition from aberrant members of the Boselaphine group into primitive oxen such as Proleptobos (Pilgrim, 1925, p. 216).

The classification of the genera contained in this family is extraordinarily difficult, and, since the systematic position of many living genera is open to doubt, that of the less perfectly known fossil genera is even more a matter of conjecture, so that any hard and fast diagnoses of the groups are obviously out of the question. The difficulty is largely increased when, as frequently happens, frontlets are
unassociated with teeth. Size is sometimes a guide to the reference of particular teeth to the frontlet in question, but when, as often occurs, two or more species are of the same size, the reference of the teeth to their respective owners must be largely guess-work. Still more extensively is this so with mandibles, which are but rarely found in association with skulls. Even in the case of the mandibles which Gaudry, in his now classic memoir on the fossils of Pikermi, referred to definite species, it is by no means certain that any greater value is to be attached to the identification. None-the-less some palaeontologists have tended to regard them as type-specimens, so that it may not be amiss to draw attention to the point. Mr. de Mecquenem has arrived at the same conclusion, although in his memoir he has seldom expressed his disagreement with the association which Gaudry or others have proposed, even where, as he has informed Dr. Pilgrim personally, his views on particular mandibles are quite definite.

Apart from such uncertainties, however, one cannot but arrive at the conclusion that the evolution of the various lineages has proceeded on such parallel lines that it will be difficult to find divergent characters of value for classification. Such characters do not seem to have been discovered yet. Numerous examples of the truth of this will be apparent to every student of the family.

First, as regards the height of the tooth crowns, no statement can be more than comparative. It is clearly recognized that originally the molars were brachyodont, and that hypsodonty was only acquired later, but more or less rapidly in different cases. None of the Pontian antelopes is fully hypsodont ; all that can be said is that certain groups, or it may be genera in a group, are conservative in this respect and others progressive. It is therefore certain that the height of the tooth-crowns has no real value in the diagnosis of a group, since the evolutionary history of this character must reveal a gradual transition from quite brachyodont to hypsodont forms. The only help which this character can give is in the case of groups in which the progress towards hypsodonty has been either exceptionally retarded or precociously accelerated.

The bending down of the face on the basi-cranial axis is a sign of advancing development, and as an aid to classification has no greater value than the degree of hypsodonty.

In a very similar category must be placed the twisting of the horn-cores. Such twisting, absent originally, has occurred in different genera at different rates. Torsion per se is not confined to particular groups, although it may have begun earlier, or be more frequent, in certain groups than in others.

In this connection it may be as well to state the convention adopted in the following pages to explain the direction of torsion. It seems less ambiguous to describe this as clockwise or counter-clockwise rather than as to the right or to the left, outward or inward. Since, however, the torsion for one of the two horns will be clockwise and for the other counter-clockwise, it is necessary to choose one horn, according to this convention the right, and to designate the torsion for this horn as characteristic for the particular species which is being considered.

The terms " close spiral " and " open spiral " have been used by many authors
in describing the mode of twisting of the horns. To remove any uncertainty as to the exact meaning of these terms when used in the following pages, it may be weli to explain that in describing a spiral as "close" we imply that the axis round which the spiral revolves passes through or near the centre of the horn, whereas in an "open spiral " the axis lies outside the actual horn. It is obvious that there may be every gradation between the two types, and the spiral of a horn may, perhaps, be not inappropriately described as " almost open" when the axis of torsion lies near the margin of the horn, or as " moderately open" when it lies nearer, but still remote from the centre of the horn. Of the various horns referred to in this work, those of Palaeoreas and Helicotragus represent the two extremes of "close" and "open" respectively.

The basicranium, which might afford sounder data for classification, is generally very imperfectly preserved. Attention will, however, be paid to the size and shape of the tympanic, to the glenoid fossa, and to the shape of the temporal cavity where these can be observed.

In these circumstances it has been thought best to adhere to the arrangement of "groups"--here termed subfamilies-and genera adopted by Schlosser in the revised edition of Zittel, "Grundzüge der Paläontologie," I923, with which we agree except as regards the genus Helicotragus, which we place in the subfamily Gazellinae instead of in the Tragelaphinae, the position which it occupies in Zittel. The family and subfamily diagnoses have been copied from the English edition of that work, in order to save the reader trouble, and must be taken with the caution expressed in a previous paragraph.

The species Tragocerus valenciennesi and Protragelaphus zitteli are made the genotypes of the new genera Graecoryx and Hemistrepsiceros respectively. Palaeoryx parvidens is the genotype of Microtragus Andree. The reasons for these modifications are noted in the appropriate places.
iv. Distribution.-Since some of the species found by Major in Samos have not been rediscovered by later workers, and since Major's names are here carefully revised in the light of subsequent work, it will be of service to attach a list of Pontian species of Bovidae, showing how far the same species occur in the more important localities for Pontian fossils. In this respect the lists given by Schlosser and Andree are both incomplete and inaccurate. The occurrence of what appear to be identical forms in such widely separated regions, not only confirms the general opinion that these deposits do not differ appreciably in age, but indicates that those regions were included in an extensive geographical province, within which the environment varied but little, and the hindrances to migration were unimportant.

The name Pontian was coined by Marny in 1869, " Géologie de Cherson." It is derived from Pontus, The Black Sea. Beds to which this term is applied are regarded as being either Upper Miocene or Lower Pliocene in age. British and French geologists incline to the latter view. The former is that held generally by other geologists.


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| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Hippotraginae. |  |  |  |  |  |  |  |  |
| Microtragus parvidens (Gaudry) .. | - | - | - |  | - | - | - | - |
| parvidens var. schafferi Andree | - | - | - | $\times$ | $\times$ | - | - | - |
| parvidens var. gaudryi n. var. | - | - | - | $\times$ | - | - | - | - |
| ? M. stützeli (Schlosser) .. | - | - | - | - | $\times$ | - | $\times$ | - |
| Hippotragus kopassi Andree .. .. | - | - | - | $\times$ | - | - | - | - |
| Palaeoryx ingens Schlosser .. | - | - | - | $\times$ | $\times$ | - | - | - |
| laticeps Andree . . | - | - | - | - | $\times$ | - | - | - |
| majori Schlosser | - | - | - | - | $\times$ | - | $\times$ | - |
| pallasi (Wagner) . | - | - | - | $\times$ | $\times$ | - | - | - |
| woodwardi n . sp. .. .. | - | - | - | $\times$ | - | - | - | - |
| woodwardi var. columnatus n. var... | - | - | - | ? | $\times$ | - | - | ? |
| Tragoreas oryxoides Schlosser .. | - | - | - | - | $\times$ | - | $\times$ | - |
| sp. Schlosser . . | - | - | - | - | $\times$ | - | - | - |
| Cervicaprinae. |  |  |  |  |  |  |  |  |
| Procobus brauneri Khomenko | - | - | - | - | - | - | $\times$ | - |
| melania Khomenko | - | - | - | - | - | - | $\times$ | - |
|  |  |  |  |  |  |  |  |  |
| Palaeoreas lindermayeri (Wagner) | - | - | $\times$ | $\times$ | $\times$ | - | - | - |
| Protragelaphus skouzesi Dames | - | - | - | $\times$ | $\times$ | - | $\times$ | $\times$ |
| Prostrepsiceros houtum-schlindleri (Rodl. \& Weith.) . | - | - | - | - | - | - | - | $\times$ |
| mecquenemi n . sp. .. .. | - | - | - | - | - | - | - | $\times$ |
| woodwardi $\mathrm{n} . \mathrm{sp}$. | - | - | - | - | $\times$ | - | - | - |
| Hemistrepsiceros zitteli (Schlosser) | - | - | - | - | $\times$ | - | - | - |
| Tragelaphus sp. Andree .. | - | - | - | - | $\times$ | - | - | - |

The list of localities given under each species in the systematic portion of this work often will be found to fall into two groups. The first group comprises those localities, specimens from which are present in the Museum collections, and always, whether the species is represented in the British Museum or not, the locality from which the holotype was obtained. The second group has the localities arranged under countries, each locality being followed by a reference to some paper. These localities are not represented in the Museum collections, and the reference is to the first paper in which they are recorded from that particular locality.

## SYSTEMATIC DESCRIPTION

## Family BOVIDAE.

Diagnosis.- " In both sexes, sometimes only in the male, skull with osseous appendages encased in horn-sheaths. Dentition $\frac{0 \cdot 0 \cdot 3 \cdot 3}{3 \cdot I \cdot 3 \cdot 3}$. Sometimes only two premolars present. Superior incisor and canine teeth absent. Cheek teeth selenodont, brachyodont or hypsodont. Carpus and tarsus as in the Cervidae. Chief metapodials united into a cannon bone with sharp distal median keels; lateral metapodials never complete, frequently wholly atrophied. Lateral digits present or absent." (Schlosser, 1925.)

## Subfamily GAZELLINAE.

Diagnosis.-"Skull flat or moderately arched, with lachrymal fossa and ethmoidal vacuity. Horns cylindrical or laterally compressed, recurved, only exceptionally spiral, never keeled. Teeth rarely brachyodont, usually strongly hypsodont." (Schlosser, 1925.)

## Genus GAZELLA Lichtenstein.

1814. Lichtenstein, Mag. Ges. Naturf. Fr., Berlin, VI, pp. 152, 17I-178. Non Pallas, 1769, Nov. Comm. Acad. Sci. Petrop., XIII, p. 468.
The synonymy of Gazella has been submitted to the International Commission at Washington. Strict application of the law of priority would probably necessitate the substitution of Cerophorus Blainville, 1816, for Gazella, and the transference of Gazella to the genus now known as Oryx. This course would cause much confusion, and, since the matter is still sub judice, we have adhered to the general practice of European mammalogists as explained by Oldfield Thomas (1924, Proc. Zool. Soc., pp. 345-348).

Diagnosis.-Small to medium-sized antelopes with moderately long face and brain-case ; face moderately bent down on the basicranial axis; horns moderately curved, not twisted, generally divergent, occasionally almost parallel, having the surface of the horn-core covered with more or less continuous longitudinal ribs, with cross-section almost circular or laterally compressed, not keeled; lachrymal fossa small and deep; lachrymal vacuity present ; supra-orbital foramina sunken in deep depressions, or pits; lachrymal forming a large part of the orbit, not indented by the malar ; tympanic bulla large and inflated ; dentition precociously hypsodont ; molars generally, but not invariably, devoid of basal pillars, without strong ribs.

Genotype.-Capra dorcas Linné, 1758.
Species.-Numerous species of gazelle have been recorded from beds of Pontian age. Several are insufficiently described, and have not received a specific name. Those which have been named are: G. baltavarensis Benda, G. capricornis (Wagner), G. deperdita (Gervais), G. gaudryi Schlosser, G. longicornis Andree, G. mytilinii Pilgrim, G. vodlevi Pilgr. \& Hopw., G. schlosseri Pavlow. Not all of these are represented in the British Museum collections, but accounts of those which are not so represented are given below.

Skull.-The horn-cores are placed over the orbits. They are recurved, more or less lyrate, sub-parallel or divergent, and vary in cross-section from sub-circular to elliptical or even sub-triangular.

The brain-case is comparatively short in relation to the face, which is bent down on the basi-cranial axis at an angle of $45^{\circ}$ or more. When this axis is horizontal the skull roof slopes gently forward and the descending plate of the occipital falls away sharply in a direction which is backward and downward. The frontals are relatively small with strong post-orbital processes.

The orbits are very large with projecting rims. They face outwards and only slightly forwards. The lachrymal fossa is usually short but very deep, the apparent depth being increased by the projection of the orbital rim. In certain recent species there is, occasionally, a fenestra in the outer table of the lachrymal. This feature, which exposes the lachrymal duct, has not been observed in the fossils. The supraorbital foramina are commonly large and sunken in deep pits; they are often immediately above a corresponding foramen in the roof of the orbit. The position of the infra-orbital foramen varies, but it is always pushed far forward to the region of the maxilla above the premolar teeth. The tympanic bulla is very large and inflated.

Dentition.-The salient points of the dentition of the various species are described under the appropriate headings.

## Gazella deperdita (Gervais).

1847. Antilope deperdita Gervais, C. R. Acad. Sci. Paris, XXIV, p. 8or.
1848. Antilope deperdita Gervais, "Zool. Paléont. Franç.," p. 78, pl. xii, fig. 3.
1849. Gazella deperdita Gaudry, " Anim. Foss. Mont Léberon," p. 57, pls. xi, xii, figs. 1-12.

Diagnosis.-A gazelle differing from G. capricomis (Wagner) in having horncores which approach each other for the first third of their height and which then diverge ; they are strongly lyrate.

Holotype.-The horn-core figured by Gervais (1852, pl. xii, fig. 3).
Localities.-The type locality is Cucuron. The species is also known from Mount Léberon.
G. deperdita has also been recorded from the following localities in Europe: France, Croix-Rousse, Lyon (Depéret, 1887, p. 243) ; ? Montredon, near Bize, Aude (Depéret, 1895, p. 433) ; ? Puy Courny, Cantal (Boule, 1896, p. 223). Macedonia, Veles (Schlosser, 1921, p. 47). Rumania, Taraklia, Bendery (Khomenko, 1913,
p. 120). Spain, Puebla de Almoradier, 20 Km . N. by E. of Alcazar de San Juan, New Castile (Hernández-Pacheco, 1921, p. 39). Ukraine, Grebniki and Tchobroutchi, Kherson (Pavlow, 1914, p. 183).

Remarks.-This species has never been fully described either by Gervais, or by Gaudry. The former gives the briefest mention of a horn-core, and Gaudry's account is mainly taken up with a description of an endocranial cast. There is not sufficient material in the British Museum to allow of further description.

Gaudry united G. deperdita with G. brevicornis (Roth \& Wagner) [=G. capricornis (Wagner)] from Pikermi, but Schlosser and De Mecquenem have insisted on the differences between the two. Their views are summarized below (p. 1o). Assuming the distinctness of the former either as a species or, it may be, a variety, it is widely though sparsely distributed. It has only been found in quantity in the Department of Vaucluse, France. Major has recorded it from Samos, but Schlosser failed to recognize it there, and among specimens collected by Major in that island we have seen none that would warrant the inclusion of the species in the Samos fauna.

## List of Specimens.

Note.-Except where otherwise stated the following specimens belong to the Bravard Collection from Cucuron.
26645. Three horn-cores. Cucuron. Pomel Colln. Purchased i85i.

34747, 34748, 34751, 34756, 34760, 34772, 34774. Seven horn-cores.
34757, 34758, 34759. Three frontlets and horn-cores.
49720. Part of the frontlet and horn-cores. Mont Léberon, Vaucluse. Purchased 1879.
34780. The right upper cheek dentition, well worn.
34781. $\quad P^{3}-M^{1}$.
26647. Two fragments of the mandible. Cucuron. Pomel Colln. Purchased 185 I.
34792. Part of the left mandibular ramus with $P_{4}-M_{3}$.
34794. The greater part of the left mandibular ramus.

34793, 34796, 34797, 34798, 34800, 34808. Six fragmentary mandibles.
34873. Part of the scapula.

34814, 348I5, 348I6. Portions of humeri.
34817 . The right radius.
34820, 34821 . The distal ends of two tibiae.
34822, 34823 . Two astragali.
$34824,34825,34826,34827,34828$. Astragalus, calcaneum, naviculo-cuboid, and two metatarsi.
34835. Axis.

34847, 34848. Two calcanea.
3488I, 34882, $34883,34884,34885,34886,34887,34888,34889,34890$. Phalanges.

## Gazella capricornis (Wagner).

1848. Antilope capricornis Wagner, Abh. Bayer. Akad. Wiss., V, Heft 2, p. 368, pl. iv, fig. 6.
1849. Antilope brevicornis Roth \& Wagner, Abh. Bayer. Akad. Wiss., VII, p. 452.
1850. Gazella brevicornis Gaudry, " Anim. Foss. Attique," p. 299, pls. lvi, lvii.

Non G. capricornis Rodler \& Weithofer, 1890, Denkschr. Akad. Wiss., Wien, LVII, p. 767.
Diagnosis.-A gazelle with horn-cores sub-parallel, curvature variable but never very strong, cross-section circular or sub-circular. Lower molars with basal cuspules.

Holotype.-The horn-core described and figured by Wagner (i848, pl. iv, fig. 6). It is preserved in the Palaeontological Museum at Munich.

Nomenclature.-This species is commonly quoted under the name of Gazella brevicornis (Roth \& Wagner). In giving it this name the authors made the comment, " die Umänderung des Namens von Antilope capricornis in A. brevicornis haben wir vorgenommen, weil denn doch die Hörner dieser Antilope nicht die eigentliche Ziegenform besitzen und nunmehr bei Pikermi eine Spezies mit wirklichen Ziegenhörnen entdeckt worden ist." This is not a valid reason for the change and the older name must be adopted.

Localities.-The type-locality is Pikermi. Specimens from Concud have also been referred to this species.

Under the name $G$. brevicornis the species has been recorded from the following localities in Europe: Euboea, Achmet Aga (Woodward, Igor, p. 485). Hungary, Baltavár, Komitat Vas (Pethö, 1884, p. 68) ; Polgárdi, Komitat Fejér (Kormos, I9II, p. 187). Macedonia, Veles (Schlosser, 192I, p. 46). Rumania, Gaiceana, Tecuci (Athanasiu, 1907, p. 13I) ; Taraklia, Bendery (Khomenko, 1913, p. I20) ; Zorleni, Tutova (Simionescu, J, 1904, p. 7I).

Remarks.-Gaudry ( 1873, p. 62) was inclined to regard the Pikermi gazelle as merely a race of $G$. deperdita, as found at Léberon and other localities in Vaucluse, Southern France. In this opinion he has been followed by Lydekker (I885, p. 5I) and Major. Schlosser (I904, p. 65), however, considered that the specific separation of the Pikermi and Léberon gazelles was justified by the triangular cross-section of the horn-cores in G. deperdita as opposed to its regularly oval shape in the Pikermi G. capricornis. He also mentions the smaller degree of curvature in the horn-cores of $G$. capricornis. De Mecquenem (1925, p. 30) has also kept them distinct, pointing to the generally greater length and divergence of the horn-cores in G. capricomis. The curvature of the horn-cores seems to be a variable character, but the other differences referred to are more constant. It therefore seems advisable to distinguish these forms by two names, though whether as distinct species, or as two varieties of the same species, must be a matter of opinion.

The remains of gazelles from Concud are very fragmentary. They appear to represent a form which had smaller horns than either G. deperdita or G. capricornis. The cross-section of the horn-cores is more compressed laterally than in G. capricomis and has not the sub-triangular outline of $G$. deperdita. The horn-cores are even smaller than in G. gaudryi Schlosser, and their longitudinal ribs are less regular. A mandibular ramus (M 8305) agrees very well with G. capricomis both in size and
dental structure, and is clearly distinct from G. gaudryi in its stouter and more complicated premolars. The remains may, therefore, be provisionally referred to G. capricornis until better material affords grounds for a certain determination. This course has already been taken by Woodward (I903, p. 206).

## List of Specimens.

Note.-The following are all from Pikermi. Except where otherwise stated they belong to the Woodward Colln.

M II440. Skull, rather badly crushed laterally and lacking the tips of both horn-cores as well as the premaxillary region.
M II442. Three frontlets with horn-cores.
M iI 443. Two frontlets with horn-cores.
M ir444. Frontlet with horn-cores on the two sides unequal.
M 13005. Skull, lacking the greater part of the face, but the frontals with the horn-cores are well-preserved, as well as the occiput. History uncertain.
34758, 34759, 38145. Three frontlets with horn-cores.
M II44I. Two palates showing the complete cheek dentition.
M I3019. Fragment of maxilla with $M^{1}$ and $M^{2}$ almost unworn.
M I3020. Right maxilla of a young individual with $d m^{3}$ and $d m^{4}$ in place and $M^{1}$ and $M^{2}$ almost unworn.
M II445. Mandible with the complete dentition, lacking only the ascending ramus ; the two rami crushed out of their natural position.
M II446. Right mandibular ramus with a small $P_{2}$.
Min482. Lower incisor teeth.
M II490. Left mandibular ramus with $P_{3}-M_{3}$; in the same slab as a maxilla of Hipparion.
MII503. Right mandibular ramus of a young individual with $d m_{4}$ in place and $M_{2}$ just being cut.
MII504. Right mandibular ramus with complete cheek dentition in a medium stage of wear.
M I3014. Left mandibular ramus with complete cheek dentition in an early stage of wear.
M 13015. Right and left mandibular rami with the premolar series, particularly $P_{2}$, relatively a little smaller than the preceding.
M I3016. Right mandibular ramus, also with a small $P_{2}$ which is represented by its root.
M 13017. Left mandibular ramus with $P_{3}-M_{2}$.
49716. Right mandibular ramus with $P_{3}-M_{2}$. Purchased 1879 .

M II462. Right hind foot.
Min463, Min464. Imperfect specimens of associated tibia, tarsus, and metatarsus.
MII465. Tarsus.
M II466. Portions of humerus.

M iI468. Distal ends of tibia and fibula, tarsus and metatarsus.
M ir 469 . Metacarpus.
Mis489. Four imperfect femora.
Mir488. The radius, ulna, and carpal bones.
Note.-The following specimens from Concud are provisionally referred to this species. Except where otherwise stated they belong to the Woodward Colln.

M 8303. Five fragmentary horn-cores.
M 10093. Horn-core. Purchased 1906.
M 8304. Maxilla with two molars.
M Ioog4. Fragmentary maxilla with molars. Purchased 1906.
M 83II. Astragalus.
M roog6, M ioo97, M roog8. Three astragali. Purchased 1906.
Gazella gaudryi Schlosser.
(PI. I, figs. I, $1 a$; pl. II, fig. I.)
1904. Gazella gaudryi Schlosser, Beitr. Paläont. Geol. Ocst.-Ung., XVII, p. 66, pl. xiii, figs. I-4.

DiAgnosis.-A gazelle with horn-cores from 20 to 30 mm . apart ; curved backwards and slightly outwards; cross-section elliptical; surface covered with deep longitudinal furrows which extend to the tip. Premolars more primitive and relatively shorter than in Gazella capricornis.

Lectotype.-The frontlet with horn-cores figured by Schlosser (i904, pl. xiii, figs. $1 a-c$ ) is hereby selected as the holotype of the species. It is preserved in the Palaeontological Museum at Munich.

Localities.--The type locality is Samos.
The only other locality in Europe is Baltavár (Benda, 1927, pp. 46, 49, 79, 80).
Remarks.--Of the two species of gazelle which Schlosser found in his Samos material, he distinguished one as Gazella gaudryi and the other as Gazella sp. The horn-cores of G. gaudryi differ from those of G. capricornis in their more elliptical section, in the greater frequency of the ribs covering their surface, and in the persistence of the ribs from the base to the tip of the horn. In addition the premolar series is not only relatively shorter than in G. capricornis, but the structure of the premolars is more primitive ; especially that of the lower premolars; the upper molars lack the basal pillar of G. capricornis ; the talon of $M_{3}$ is triangular instead of rounded.

So far as the teeth are concerned there is a well-preserved mandible ( $\mathrm{M}_{4} 177$ ) in the Major collection, of which the left ramus is figured in Pl. II, fig. I, as well as an isolated left ramus (M4176). Both agree well with the specimens figured by Schlosser. A right maxilla with $P^{2}-M^{2}$ (M 419I) also agrees with the upper teeth figured by Schlosser. The collection contains no adult skull or isolated horn-cores which belong to this species.

There are in the British Museum collection three frontlets (M 4173-5) of which the one figured (Pl. I, fig. I) is the best preserved. They all possess divergent horn-cores
of small size, only slightly compressed laterally, and with ribs running regularly along the whole length of the horn. The horn-cores are, however, situated extremely far apart on the frontal, which is also narrower than in normal G.gaudryi. The small size and greater spacing of the horn-cores are easily explicable on the assumption that we have before us three young individuals. If, on the other hand, the frontlets belong to adults, their possessors must have had smaller teeth than those just mentioned as agreeing with G. gauddryi. There are, however, no teeth of such dimensions in the collection. I think, therefore, that the frontlets are most reasonably regarded as young individuals of $G$. gaudryi. It is, however, quite possible that they are adults of another species with widely spaced horns, somewhat allied to G. muscatensis. In this case they represent a new species, and it may be that these are the specimens on which Major (1894, p. 4) founded one of his species of Gazella.

## List of Specimens.

Note.-The following specimens all belong to the Major Collection from Samos.
M 4173. Skull of a young (?) individual, complete from the horn-cores to the occipital condyles, but much crushed from above and the teeth lost.
Length from posterior base of horn-cores to occipital crest 52 mm .
M 4I74. Left side of frontlet of young (?) individual with horn-core.
M 4 I 75 . Frontlet of young (?) individual with horn-cores (Pl. I, fig. I).

| Length of horn-core |  |  |  |  |  |  | 43 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Sagittal diameter of horn-core |  |  |  |  |  |  | 17 |
| Transverse diameter of horn-core |  |  |  |  |  |  | 14 |
| Distance between horn-cores at base |  |  |  |  |  |  | 29 |

M 419I. Right maxilla with $P^{2}-M^{2}$.
M 4176. Left mandibular ramus with $P_{2}-M_{3}$; slightly larger than the following.
M 4I77. Almost perfect mandible with complete dentition (Pl. II, fig. I).
Length from $I_{3}-M_{3} \quad . \quad$. .. .. .. .. .. .. .. $\quad$ mm.
Length of premolar series .. .. .. .. .. .. .. .. I7
Length of molar series .. .. .. .. .. .. .. .. 35
Length of diastema between $P_{2}$ and $I_{3}$.. .. .. .. .. .. I6
Depth of jaw beneath $M_{3}$ (measured on outside) .. .. .. .. .. 19
M 4179. Distal end of tibia, metatarsus, tarsus and phalanges. (Provisional reference.)

## Gazella mytilinii Pilgrim.

$$
\text { (PI. I, figs. } 3,3 a, 3 b \text {.) }
$$

1904. Gazella sp. Schlosser, Beitr. Paläont. Geol. Oest.-Ung., XVII, p. 68, pl. viii, fig. 7 ; pl. xiii, figs. 5, 6, 8, 9 .
1926, Sept. Gazella schlosseri Andree, Palacontographica, LXVII, p. 168, pl. xvi, figs. 2, 4, 5, 8. non G. schlosseri Pavlow, 1913, Nouv. Mém. Soc. Nat. Moscout, XVII, liv. 3, p. 19, pl. ii, figs. 1-13.
1926, Nov. Gazella mytilinii Pilgrim, Ann. Mag. Nat. Hist., (9), XVIII, p. 464.

Diagnosis.-A gazelle in which the hinder half of the orbit is situated beneath the horn-core. Horn-cores parallel, with elliptical cross-section; curvature backwards and but very slightly outwards ; longitudinal furrows very unequal in length and breadth, none of them extend from the base to the tip. $P^{2}-P^{3}$ larger than in G. gaudryi; basal pillars wholly lacking.

Lectotype.-The skull described and figured by Andree (1926, pl. xvi, figs. $2,4,5,8$ ) is hereby selected as the holotype of the species. It is preserved in the State Museum of Natural History at Vienna.

Localities.-The type locality is Samos.
The species is also recorded from Rumania, Taraklia, Bendery (Khomenko, 1913, p. 121).

Nomenclature.-The name is taken from Mytilini the village in Samos near which Major's specimens were found, and not from Mytilene the capital of Lesbos.

Andree's name for the species, G. schlosseri, is preoccupied by Professor Marie Pavlow for a South Russian species of gazelle which was described in 1913, and which is noticed below.

Remarks.-In the Major Collection are eight mandibular rami (M 4I8I-4I85) and two maxillae (M4180, M I3024) which appear to correspond almost exactly with Schlosser's figures and descriptions. There is also a frontlet ( $\mathrm{M}_{5420}$ ) from Samos in which the left horn-core is perfect, whereas the right horn-core is broken off near the base. This specimen (Pl. I, figs. $3,3 a, 3 b$ ) is extremely close to the Munich skull, the horn-cores differing only in their slightly greater lateral compression, and it is quite impossible to separate the two.

Andree (1926, p. 168) says that the teeth of the holotype agree very well with those of G. gaudryi both in construction and size, with the exception that $P^{2}$ and $P^{3}$ are somewhat larger, and that basal pillars are wholly lacking. For this reason he disagrees with Schlosser regarding the identification of the teeth described by the latter. For the time being, however, we have thought it best to adhere to Schlosser's account and to refer the odd specimens of teeth mentioned above to G. mytilinii.

As Schlosser has remarked, the resemblance of G. mytilinii to G. deperdita and G. capricomis is not very close, both on account of the narrowly elliptical outline of the cross-section of the horn-cores as well as of the very trifling degree of divergence. From G. gaudryi the present species differs, not only in its larger size, but also in the parallelism of the horn-cores, and in the fact that the ribs are quite irregularly distributed on the surface and do not run from the base to the tip. G. porrecticornis from the Pontian of India differs in the much greater divergence of the horn-cores.
G. mytilinii seems to be much nearer to G. vodleri Pilgr. \& Hopw., olim G. capricornis Rodler \& Weithofer, but both in the holotype of that species, as well as in the specimen from Maragha figured by De Mecquenem (1924, pl. iii, fig. 3), the outward curvature of the horns in their upper third seems to be much more pronounced. The specimen in the British Museum ( M 5420 ) hardly shows such a curvature at all, although it appears to be present in some degree in the Munich skull, provided that that specimen is not distorted.
G. dorcadoides and G. palaeosinensis of the Chinese Pontian are regarded by

Schlosser (1903, pp. 130, 133) as related respectively to the recent G. dorcas and G. subgutturosa. In that case they are considerably removed from the Samos species. G. altidens Schlosser (1903, p. r3r) from the Pontian of China has, presumably, much more hypsodont teeth than G. mytilinii; they are certainly more hypsodont than those in the British Museum mandibles. Gazella schlosseri (Pavlow, 1913, p. 19) from Rumania differs by reason of its less compressed, less curved, and more divergent horn-cores. Of the species attributed by del Campana (r918, pp. 151-2Io) to the genus Gazella, G. gracillima Weit. from Monte Bamboli is only about half the size of the Samos species, and is considered by him to show affinities to the recent genera Cephalophus, Oreotragus, and Madoqua. In G. fucinii del Campana the horn-cores are not only more curved, but their cross-section is much more nearly circular. G. haupti Major has lyre-shaped horns, and it is very doubtful whether it can be placed in this genus at all.

Of the gazelles of the younger Pliocene and Pleistocene, G. borbonica Depéret (I883-4, p. 25I) has more upright as well as much longer and stouter horns. G. anglica Newton ( 1884, p. 280) has much more compressed and less curved horn-cores. G. daviesii Hinton (1908, p. 445) has much smaller and still more compressed horncores. The fossil antelopes from Algeria, originally described by Pomel (1894), are considered by Joleaud (r917, pp. 208-225) to be referable to recent African species of the group of $G$. dorcas and G. cuvieri. The one which seems to stand nearest to $G$. mytilinii is $G$. ovanensis Pomel. It is probable that this cannot be distinguished from $G$. rufifrons var. rufina. The divergence of the horn-cores and the shape of the supra-orbital pits seems to be the same, but the Algerian species has more compressed horn-cores. G. atlantica Thomas (1884-5, p. 17), also from the Pleistocene of Algeria, has horn-cores which are more compressed than they are in the Samos gazelle.

Among living species the nearest to G. mytilinii is G. thomsoni. Not only is that a smaller species, but the horn-cores are narrower and the position of the supraorbital pits differs, being rather inside than in front of the horn-cores. G. granti is a much larger species. It is characterized by extremely deep supra-orbital pits.

## List of Specimens.

Note.-The following specimens from Samos all belong to the Major Colln. except M 5420 .

M 5420. Frontlet with perfect left horn-core ; the right horn-core broken near the base (Pl. I, figs. 3, $3^{a}, 3^{b}$ ). Purchased 1894.


M 4180. Right maxilla with cheek dentition in an advanced state of wear ; crown of $P^{2}$ imperfect.
M 13024. Left maxilla with $M^{1}-M^{3}$ in an advanced state of wear.


Gazella baltavarensis Benda.
1927. Gazella baltavarensis Benda, "A Baltavári Öslénytani Ásatások 70 Éves Története," p. 46, No fig.
Diagnosis.--" . . . Closely allied to G. brevicornis [i.e. G. capricomis (Wagner)]; horn-core greatly thickened, without furrows (lit. 'wrinkles smoothed'). Horncores very obtuse and blunt. . . . Dentition closely resembling that of G. gaudryi."

| Dimensions of Teeth in millimetres- |  |  |  | $P_{2}$ | $M_{1}$ | $M_{2}$ |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Length | $\ldots$ | $\ldots$ | . | $\ldots$ | $\ldots$ | . | $5 \cdot 3$ | $5 \cdot \mathrm{I}$ | $4 \cdot 9$ |
| Breadth | $\ldots$ | $\ldots$ | . | $\ldots$ | . | .. | $3 \cdot \mathrm{I}$ | $2 \cdot 8$ | $2 \cdot 8$ |

Locality.-The type locality is Baltavár. None other is recorded.
Remarks.-The preliminary account from which the above particulars are translated is not sufficient to enable the species to be recognized. Dr. Benda intends to publish further details in Földtani Közlöny, LVII, 1927.

## Gazella longicornis Andree.

1926. Gazella longicomis Andree, Palaeontographica, LXVII, p. 169, pl. xvi, figs. 3, 9.

Description.- "The forehead is deeply excavate in front of the horn-cores, much as in $G$. schlosseri n. sp. [i.e. G. mytilinii Pilgrim]. The nasals terminate in an acute-angled suture. Of the skull sutures only the frontal is moderately thickened in its hinder part towards the fronto-parietal. The latter runs practically at right angles to the long axis of the skull. The orbits lie one-third in front of the bases of the horn-cores.
" The horn-cores are long, standing up well as in G. gaudryi Schl., regularly and not strongly curved backwards. Their transverse section is elongate-elliptical, the divergence fairly considerable." (Andree, transl.)

Holotype.--The frontlet and horn-cores described and figured by Andree ( 1926 , pl. xvi, figs. 3, 9). It is preserved in the Geological Institute at Münster.

Locality.-The type locality is Samos. None other is recorded.
Remarks.-Andree regards this species as being near to G. gaudryi Schlosser, from which he differentiates it by its much longer horns, and more deeply excavate forehead.

## Gazella rodleri nom. nov.

1890. Gazella capricornis Rodler and Weithofer, Denkschr. Akad. Wiss. Wien, LVII, p. 767, pl. v, fig. I, pl. vi, fig. 6.
Non G. capricornis (Wagner), 1848, Abh. Bayer. Akad. Wiss., V, p. 368, pl. iv, fig. 6.
Description.- " In comparison with Gazella deperdita the bases of the horncores are appreciably nearer the middle line of the skull, and diverge very little in their lower third, above which they turn rapidly outwards. The orbital margins project somewhat laterally and have the horn-cores placed over them in the Gazelle manner. At the bases of the horn-cores, somewhat internal to them, are the large supra-orbital foramina, between which the forehead is depressed. A weak sagittal crest is present.
" The horn-cores themselves are strongly compressed laterally. The anterior end of the major diameter of the ellipse is antero-internal [at the base of the horn] becoming more external as it is traced upwards [towards the tip], so that the horn thereby becomes warped and twisted, and thus reminiscent, to a significant degree, of that of the goat. There are no grooves [on the surface]. The horn-core tapers rapidly towards the apex."
"The points of difference from Gazella deperdita are thus very striking. They consist in the oblique insertion and entirely different form of the horn-cores." (Rodl. \& Weit., transl.)

Localities.--The type locality is Maragha.
In Europe the species has been recorded from Rumania, Taraklia, Bendery (Khomenko, 1913, p. I20).

Remarks.-The name originally allotted to this species was preoccupied by G. capricornis (Wagner), 1848, hence the change.

## Gazella schlosseri Pavlow.

1914. Gazella schlosseri Pavlow, Ann. Géol. Minér. Russie, XVI, livr. 7-8, p. 183, pl. viii, figs. 6, 7 .

Diagnosis.-" It is distinguished by its slender, erect and grooved horn-cores ; the grooves extend along the horn-core to the summit. The cranial vault is rounded. $P_{4}$ has an accessory tubercle on the inner face of the anterior half." (Pavlow, transl.)

Holotype.-The skull figured by Pavlow (I914, pl. viii, fig. 6). It is preserved in the Geological Cabinet of the University of Moscow.

Locality.--The type locality is Grebniki, Kherson, Ukraine. None other is recorded.

## Gazella spp. Auctorum.

In addition to the species mentioned above, various authors have described in more or less detail parts of skulls, dentitions, or skeletons of Gazelles. These have been given the designation Gazella sp. or else a variant on that. As a rule the remains described under these headings are of no importance, but attention may be directed here to two examples described and figured by Andree (1926, p. 168, pl. xvi, figs. 2, 4, 5,$8 ;$ p. 169 ). They were found in Samos, and are both preserved in the Geological Institute at Münster.

Gazella, n. sp. ? Andree.
1926. Gazella n. sp. ? Andree, Palaeontographica, LXVII, p. 168, pl. xvi, figs. 2, 4, 5, 8.

Description.-." The excavation of the forehead in front of the horn-cores is unimportant; the frontal suture is very slightly swollen; the fronto-parietal suture appears not to be thickened."
" The horn-cores are inserted very obliquely on the skull, and are regularly but slightly bent backwards. The furrows are irregular and only one, deeper than the rest, on the hinder surface runs up to the summit. The feature which distinguishes the new species from all others previously known from Pikermi and Samos is the turning inwards of the tips of the horn-cores." (Andree, transl.)

## Gazella (sp.) Andree.

1926. Gazella Andree, Palaeontographica, LXVII, p. r69, text-fig. 4.

Description.-" The horn-cores are most like those of G. gaudryi Schl. They are not long, little curved, and have fairly regularly disposed furrows. Their crosssection is elliptical, and the divergence not great. . . . The horn-cores are, however, very obliquely placed on the skull in contrast to G. gaudryi Schl. Further, half of the orbit lies in front of the base of the horn-core. The present fragment is distinguished from G. deperdita Gaudry and G. schlosseri n. sp. [i.e. G. mitylinii Pilgr.] by the weak curvature of the horn-cores and their almost regular furrowing, from G. brevicornis Gaudry [sic., err. pro G. brevicornis (Roth \& Wagner), i.e. G. capricornis (Wagner)] by the elliptical cross-section of the horn-cores, and from capricomis Rodl. \& Weith. [i.e. G. rodleri Pilgr. \& Hopw.] by the lack of torsion in the horn-cores. Identification is not possible with Gazella n. sp. and longicornis since the one species has horn-cores which are turned inwards, and the other horn-cores which stand erect." (Andree, transl.)

## Genus HELICOTRAGUS Palmer.

1888. Helicoceras Weithofer, Beitr. Paläont. Geol. Oest.-Ung., VI, p. 288, pl. xviii, figs. r-4. Non D'Orbigny, 1842, " Paléont. Franç., Terr. Cret.," I, p. 6 ri.
1889. Helicophora Weithofer, Jahrb. geol. Rchsanst. Wien., XXXIX, p. 79, footnote. Non Gray, J. E., r842, "Syn. Cont. Brit. Mus.," p. 59, 89.
1890. Helicotragus Palmer, Science, n.s., XVII, p. 873.

Diagnosis.-Antelopes with a very short face and cranium ; possessing spirally twisted horn-cores, forming an open spiral of about one revolution, with a circular cross-section, keels weak, or obscurely present, horn-cores strongly tilted backward ; face either very slightly or rather considerably bent down on the basicranial axis; frontal extremely short and broad; supra-orbital rims projecting; supraorbital foramina. very small, lying at postero-external corner of a broad shallow depression; lachrymal entering very little into the composition of the orbit; lachrymal fossa deep ; tympanic bulla moderately large.

Genotype.--Helicoceras rotundicome Weithofer (1888, p. 288).
Nomenclature.-The earliest known species of this genus was described by Weithofer in 1888, from Pikermi material, under the name of Helicoceras rotundicorne. The name Helicoceras being preoccupied by D'Orbigny (1842) for a genus of Mollusca, Weithofer replaced it in 1889 by Helicophora. Palmer (1903) pointed out that the latter also had been preoccupied for a Molluscan genus by Gray (1842). He therefore replaced it by Helicotragus. The change was adopted by Trouessart in the Supplement to his "Catalogus Mammalium" but seems to have escaped the notice of all subsequent writers, including Schlosser (I904), the authors of the revised edition of Zittel's "Grundzüge" (1923), and Andree (1926). Helicotragus appears to be the correct designation of the genus.

Species.-In addition to the genotype there is one other known species. This was described and figured by Andree (Sept. 1926) under the name Helicoceras fraasii.

Skull and Dentition.-The horn-cores, which are markedly lyrate, are circular in cross-section with one ( $H$. fraasii) or two ( $H$. rotundicornis) keels. The keels are very slight. The horn-cores form an open spiral in a clockwise direction. This spiral involves at most one revolution. The horns twist round a central axis but at a much greater distance from it than in any Tragelaphine, and this gives them an altogether different appearance from the horn-cores of either Prostrepsiceros, Protragelaphus, or Palaeoreas. In these genera the axis of torsion lies within the horn, either near its centre as in Palaeoreas, or near its margin as in Prostrepsiceros woodroardi.

Of the characters of the face and brain-case very little is known. The braincase of $H$. fraasii has been described shortly by Andree (r926, pp. r63-164) and this account is followed here. One specimen in the British Museum preserves a few details of the upper part of the face. This specimen ( M r1437) is all the evidence at present known which concerns the face and the tympanic region.

The brain-case seen from above has a nearly square outline. The fronto-parietal and frontal sutures are swollen. This is especially well marked in the frontal suture which forms a strong ridge separating the horn-cores as well as the supra-orbital fossae. A part of the supra-occipital takes part in the formation of the roof of the brain-case. It is slightly elevated with respect to the other bones. Two longitudinal crests arise at the bases of the horn-cores where they abut on the frontoparietal suture and pass backward to the suture between the parietals and the supraoccipital. The occipital bone falls away obliquely from the roof of the skull at an approximate angle of $\mathrm{II} 5^{\circ}$. It has a definite vertical crest in the centre line. The condyles appear to be comparatively large. The tympanic bulla is large and inflated. It resembles that of the Gazelles and, even more closely, that of Antilope cervicapra. The bulla is much smaller in the Ovicaprinae, and much larger in the Tragelaphinae. Measured between the nasal and parietal sutures the frontals are remarkably short. They bear on their surface the broad and shallow frontal fossae, above and close to the superior external borders of which the supraorbital foramina open. The foramina themselves are extraordinarily small.

The facial portion of the skull is practically unknown. It seems that it was very short. The nasals and the lachrymals in their upper portions resemble the corresponding structures in the Indian Black Buck (Antilope cervicapra). In both animals the molar indents the lachrymal acutely. That portion of the latter which abuts on the orbit is as small, or smaller, than the corresponding portion in A. cervicapra. Its relations thus differ markedly from those in the tragelaphines and gazelles. There appears to be a vacuity between the frontal, nasal, and lachrymal bones. The lachrymal fossa is deep.

No skull of Helicotragus yet described has the dentition preserved. In consequence there is a strong element of uncertainty in the attribution of isolated sets of teeth to this genus. If we may judge $H$. rotundicornis by its similarity to Antilope cervicapra and by the identical size of the glenoid in both, we should not expect the teeth to be any smaller than they are in the recent species. On account of the proportionately broader forehead in the fossil, they might, indeed, be bigger. As
with all the Pontian antelopes, the teeth may be expected to be more brachyodont and broader than in the recent form. We conceive, therefore, that in size and general character they may resemble those of Palaeoreas. Possibly this resemblance has prevented their recognition. Schlosser (1904, p. 72) has figured some isolated teeth which, he says, are too big for Gazella deperdita and much too small for Palaeoreas lindermayeri, and he suggests that they may belong to Helicotragus. The teeth in question are certainly a little smaller than those which are referable to Palaeoreas, so that there is nothing unreasonable in Schlosser's suggestion; but in any case their resemblance to Palaeoreas is close, and the reference is still entirely conjectural.

Affinities.-De Mecquenem (1925, p. 39) is inclined to consider Helicotragus a close ally of Oioceros and to class it with the Ovicaprinae. It is true that the orbital rims project equally far outside the horn-cores, but the direction of torsion of the horns is opposite in the two genera, being clockwise in Helicotragus and counter-clockwise in Oioceros. In addition, the length of the frontal, the absence of a fossa into which the supra-orbital foramina open, the absence or smaller size of the lachrymal fossa, and, finally, the small size of the tympanic bulla, all clearly distinguish the Ovicaprinae from Helicotragus. This genus is, however, just as far removed from the Tragelaphinae, from which it differs in its projecting orbits, short frontals, marked supra-orbital fossae, the entirely different shape of the occipital, the smaller tympanic bullae, and the different characters of the glenoid.

The close resemblance between the skull of Helicotragus and that of Antilope cervicapra can hardly be fortuitous. The skull is shorter than that of A. cervicapra in the parietal and occipital regions. The horn-cores differ in the two genera merely by the fact that in Helicotragus there is slightly more trace of the keels. In $H$. rotundicornis the face is less bent down on the basicranial axis than in A. cervicapra. This it is true is a character which might be expected in a Pontian ancestor ; nevertheless in the species $H$. fraasii the angle between the facial and basi-cranial axes is quite as acute as it is in the recent species. No doubt we have in H. rotundicornis an animal which has a greater claim to be regarded as the ancestor of A. cervicapra than any one of the species of Protragelaphus, Prostrepsiceros, or Hemistrepsiceros has to be an ancestor of the modern Tragelaphinae. We do not, however, regard that species as the direct ancestor of the modern Indian antelope because of the slight keels on the horn-cores, which are not likely to have vanished as evolution proceeded. The shortness of the face and cranium and the small degree of bending down of the face on the basicranial axis do not appear to be so important, since these might very well be features of an earlier stage of evolution, and so might conceivably occur in a Pontian ancestor. It may be, however, that a marginal species of Helicotragus, without keeled horn-cores, was on the direct line of descent of $A$. cervicapra.

An isolated horn-core from the Pleistocene gravels of the Narbada in India (B.M. 37264) was catalogued by Lydekker (I885, II, p. 52) under the name of A. cervicapra. It differs from that species in the possession of a marked posterior keel and in the more elliptical cross-section; in both these respects it resembles Helicotragus, but its fragmentary nature forbids a definite reference.

The females of $A$. cervicapra are normally unprovided with horns. Since all the frontlets of Helicotragus yet known have horns, the inference might be drawn that the females of this genus were horned. It is, however, very unsafe to draw such an inference, especially in the absence of teeth. As an example of a mistaken conclusion of this nature, based on even better evidence, may be cited Gaudry's opinion, founded on the presence of twenty horned skulls of Tragocerus amalthea in his Pikermi collection, that the females of this species possessed horns. Later observations by Dames and Weithofer proved that this opinion was unsound. So in the case of Helicotragus, it is at least possible that the females were hornless; but, even if this were disproved, it would not necessarily disturb the taxonomic position of the genus. In certain species of Gazella the females are, normally, provided with horns, whereas most species have hornless females. Schlosser, with his usual acumen, and on much less evidence than we have before us, formerly suggested (1904, pp. 86, 92, 94) the affinity of Helicotragus with the Antilopinae and a near relationship to A. cervicapra. In the latest edition of Zittel's "Grundzüge der Paläontologie" (I923), however, he seems to have altered his opinion, since the genus retains its place in the group Tragelaphinae.

## Helicotragus rotundicornis Weithofer.

> (Pl. I, figs. 2, 2a.)
1865. Palaeoreas lindermayeri pars. Gaudry, "Anim. Foss. Attique," p. 292, pl. lii, fig. 5, non fig. 4.
1888. Helicoceras rotundicorne Weithofer, Beitr. Paläont. Geol. Oest.-Ung., VI, p. 288, pl. xviii, figs. I-4.
1889. Helicophora rotundicornis (Weith.), Weithofer, Jahrb. Geol. RchsAnst., Wien, XXXIX, p. 79.
1903. Helicotragus rotundicornis (Weith.), Palmer, Science, n.s., XVII, p. 873.

Diagnosis.-A Helicotragus in which the horn-cores diverge at an angle of $7 \mathrm{I}^{\circ}$ approximately. Horn-cores with two faint keels, one arising from the posteroexternal, and one from the postero-internal corner of the horn-core, the latter often so faint as to be almost non-existent.

Lectotype.-The specimen figured by Weithofer ( 1888 , pl. xviii, figs. I, 2) is hereby chosen as the holotype of the species. His second specimen thus becomes the paratype. It is somewhat distorted by pressure. Both specimens are preserved in the Palaeontological Museum of the University of Vienna.

Localities.-Pikermi is the only definite European locality for this species. Major (189I, p. 88) records it from Samos. It is not certain on what this identification was based.

Remarks.-The most complete portion of a skull in the British Museum collection is M II437. This shows the frontal with both horn-cores, the right orbit, and the face for about 30 mm . in front of the fronto-nasal suture. The maxillae are lacking. In the hinder region of the skull a portion of the occipital near the foramen magnum is preserved. Both the upper portion of the occipital and the condyles have been broken away. The right tympanic bulla and the glenoid fossa are well shown. The right zygomatic is crushed into the side of the skull.

The horn-cores are nearly circular in cross-section with very faint keels. The existence of irregular longitudinal grooves and markings enables the spiral winding
of the horns to be followed easily. Both in their general shape as well as in the degree of torsion they agree very closely with those of Antilope cervicapra. In that species, however, their cross-section is quite circular, without the keels. The general axis of the horn-cores is inclined backward in practically the same plane as the face, and makes an angle of less than $30^{\circ}$ with the occiput. This is more acute than in Tragelaphus, and still more acute than in the fossil Tragelaphine genera here described, and than in Palaeoreas. Since the horns in the latter genus also continue in the plane of the face, the difference is due to the greater degree of bending down of the face on the basicranial axis. In the present skull the angle between the facial and basicranial axes is very obtuse ; a difference of $25^{\circ}$ would put them both in the same plane.

The frontal is extraordinarily short and broad. A list of comparative measurements and ratios serves to emphasize this.


The cranium is short, and so broken that no precise measurements are possible. It is almost certain, though, that the distance between the hinder edge of the orbit and the occipital condyle (basal portion) cannot have been much more than seventy millimetres. Corresponding values for a few other antelopes are given.

| Helicotragus rotundicornis |  |  |  |  |  |  | $\text { ? } 70$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Antilope cervicapra |  |  |  |  |  | . | 75 |
| Palaeoreas lindermayeri |  |  |  |  |  | $\cdots$ | 77 |
| Protragelaphus skousesi |  |  |  |  |  | . | 75 |
| Tragelaphus massaicus |  |  |  |  |  |  | 95 |

The parieto-occipital suture is not clearly visible, but, judging by the relation between the tympanic, the temporal, and that part of the occipital which is preserved just above the condyles, it is likely that the parietal was much shorter than in Antilope cervicapra. In general aspect the occipital and the tympanic regions resemble those of that species very closely. The differences from Tragelaphus and Protragelaphus are much greater; in both these genera the occipital condyles are situated more to the rear.

In size and shape the glenoid fossa is identical with that of Antilope cervicapra, but differs from that of Tragelaphus and Strepsiceros.

The outline of the temporal cavity, as delimited by the glenoid and the zygoma is almost rectangular in both $H$. rotundicornis and A. cervicapra, as it is in the gazelles and the Ovicaprinae, whereas in the Tragelaphinae it tapers at the postero-external corner.

The supra-orbital depressions are not so deep as they are in $A$. cervicapra, Palaeoreas lindermayeri, or Gazella. On the other hand, they are much larger than
in the modern genera Tragelaphus and Strepsiceros. They are not unlike those of the genera Prostrepsiceros and Hemistrepsiceros. The supra-orbital foramina are very small, a condition which may be correlated with a very short face.

Great uncertainty attends any effort to assign teeth to this species. There are, however, six mandibular rami in the Woodward collection which agree closely in size with Palaeoreas lindermayeri, but differ from it in their rather stouter teeth and the relatively shorter premolar series. The premolars are also simpler and in $P_{4}$ there is only one posterior wing instead of two. It seems not unlikely that these rami might find a place here.

## Material.

Note.-The following are all from the Woodward Colln., Pikermi.
M II437. Skull, complete as to the frontal region, and with the right orbit and lachrymal. Horn-cores broken off some distance below the tips; occipital region imperfect and lacking the condyles, but showing the basicranium fairly well on the right side ; teeth wanting. (Pl. I, figs. 2, 2a.)
M II436. Frontlet showing parts of both orbits ; horn-cores as in the preceding specimen ; occipital and maxillary portions wanting.
M 12999. Imperfect frontlet with horn-cores less divergent than in the two preceding specimens.
M II438. Left horn-core.
MII505. Six mandibular rami, provisionally referred to this species.

## Helicotragus fraasii (Andree).

1926. Helicoceras fraasii Andree, Palaeontographica, LXVII, p. I63, pl. xi, fig. 4, pl. xv, fig. I.

Diagnosis.-A Helicotragus in which the horn-cores diverge at an angle of approximately $96^{\circ}$. Horn-cores with only one keel.

Holotype.-The skull described and figured by Andree, which is the only known specimen. It is preserved in the Natural History Cabinet at Stuttgart ; Regd. No. 13278.

Locality.-The type locality is Samos. None other is recorded.
Remarks.-This species is slightly larger than the preceding one, and differs from it in the greater divergence of the horn-cores, as well as in the greater degree of bending down of the face on the basicranial axis. We are doubtful whether the other differences noticed by Andree, especially the strength and position of the keels, are not due to individual variation. The widely divergent horn-cores of the specimen from Maragha figured by De Mecquenem (1925, pl. vii, fig. I) suggest that it is most probably referable to this species.

## Subfamily OVICAPRINAE.

Diagnosis.-" Skull strongly arched; cranial axis strongly bent. Horns keeled, simply or spirally curved. Frontal appendages usually hollow. Lachrymal
fossa small or wanting, ethmoidal vacuity fissure-like or absent. Teeth generally strongly hypsodont and laterally compressed." (Schlosser, 1925.)

## Genus OIOCEROS Gaillard.

1857. Antilope Wagner, Abh. Bayer. Akad. Wiss., VIII, p. I54.
1858. Antidorcas? Gaudry, " Anim. Foss. Attique," p. 297.
1859. Oioceros Gaillard, Bull. Soc. Anthrop. Lyon, XX, p. 93.

Diagnosis.--Bovidae of small size with long slender muzzle; face bent down on basicranial axis either slightly or to a moderate extent ; orbits far forward, with expanded orbital roof; lachrymal fossa short, rather deep or shallow; supraorbital foramina sunken in small depressions; small lachrymal vacuity; horncores twisted counter-clockwise in a fairly close spiral of one or two revolutions, widely separate, tilted backward or fairly upright, divergent, with a cross-section almost circular or elliptical, keeled either anteriorly or posteriorly or both ; dentition moderately hypsodont, premolar series rather long and slender, molars broad with ribs of medium strength.

Geno-lectotype.-We hereby select Antilope rothi Wagner (1857, p. I54, pl. vi) as the type of the genus.

Remarks.-Five species have been referred to this genus, namely, O. rothi Wagner, O. atropatenes Rodler, O. proaries Schlosser, O. boulei De Mecquenem, O. wegneri Andree.

It will be inferred from the generic diagnosis that the species differ widely among themselves. Schlosser (r904, p. 74) has remarked that it is possible that they belong to more than one genus. We fully endorse this opinion, but since the material at our disposal is insufficient for their complete diagnosis we prefer to keep them all in the one genus for the present. Schlosser is of the opinion that the expansion of the supra-orbital roof, the counter-clockwise torsion of the horns, and many other characters, mark the various members of this genus as being related to the sheep and goats. It is because we agree with this view that we have retained the genus Oioceros in the sub-family Ovicaprinae.

## Oioceros rothi Wagner.

1857. Antilope rothi Wagner, Abh. Bayer. Akad. Wiss., VIII, p. 154, pl. vi, fig. 20.
1858. Antidorcas? rothi Gaudry, "Anim. Foss. Attique," p. 297, pl. lii, figs. 2, 3 .
1859. Oioceros rothi Gaillard, Bull. Soc. Anthrop. Lyon, XX, p. 93, fig. 8.

Diagnosis.-An Oioceros with lyrate horn-cores placed over the orbits. Horncores rounded, about 15 mm . apart at the base, flattened and subparallel at the tip. Keel extending from the external face of the base of the horn to the tip, strongly or weakly developed, torsion of keel less than that of the horn-core.

Holotype.-The specimen described and figured by Wagner (r857, p. 154, pl. viii, fig. 20). It is preserved in the Palaeontological Museum at Munich.

Locality.-The type locality is Pikermi. None other is recorded.

Remarks.-The only specimen in the collection is an imperfect frontlet, mounted on a plaster base; it preserves about two-thirds of the length of the horn-cores. That the two horn-cores were derived from the same individual is not absolutely certain.

The keel and counter-clockwise torsion of the horns are unmistakable. The specimen is too small to be referred to Oioceros atropatenes (Rodler). Moreover, the horn-core of the latter species has a more circular cross-section, and is rather less twisted than it is in the Pikermi form. The horn-cores appear to have been derived from a rather smaller individual, or individuals, than that which Gaudry has figured. On the other hand, they are considerably larger than those on the frontlet from Maragha figured by De Mecquenem (1925, pl. vii, fig. 4) and referred by him to this species.

## Specimen.

MII46I. Two horn-cores mounted on plaster. It is not certain that they belong to the same animal. Pikermi. Woodward Colln.

## Oioceros? proaries Schlosser.

1904. Oioceros? proaries Schlosser, Beitr. Paläont. Geol. Oest.-Ung., XVII, p. 73, pl. xiii, figs. Io, II, I3.

Diagnosis.-An Oioceros with the premolar series fairly long in comparison with the length of the skull. Upper molars as broad as long.

Holotype.-The skull described and figured by Schlosser (1904, p. 73, pl. xiii, figs. Ioa-IOc). It is preserved in the Palaeontological Museum at Munich.

Locality.-The type locality is Samos. None other is recorded.
Remarks.-The species was founded on a hornless female skull, and for this reason it is very difficult to ascertain its true relationships. Comparison of the upper dentition with that of the holotype of $O$. boulei De Mecquenem (1925, p. 4I, text-figs. Io, II, pl. vii, fig. 8) shows, so far as reliance on the figures is possible, that there is very strong reason to believe that the present species is correctly referred to the genus Oioceros.

The only specimen in the Major collection which can be referred to this species is a much broken, hornless skull. Most of the face is lacking, as well as the entire upper dentition.

## Specimen.

M 42I2. A poorly preserved and much broken skull. Samos. Major Colln.

## Oioceros wegneri Andree.

1926. Oioceros wegneri Andree, Palaeontographica, LXVII, p. I7o, pl. xv, figs. 3, 6.

Diagnosis.-An Oioceros with the face bent down at right angles to the basicranial axis. Facial portion of skull about twice as long as the brain-case. Orbits large, oval, much produced laterally, almost entirely in front of the base of the horncore, anterior margin over $M^{3}$. Frontal suture forming a sharp crest between the
supra-orbital foramina and the bases of the horn-cores. Horn-cores very broad at the base, placed obliquely on the frontals. Keels three in number, the strongest arising on the antero-external face of the horn-core, the two others on the anterior face, keels twisted through at least one revolution.

Holotype.-The skull described and figured by Andree (1926, p. I70, pl. xv, figs. 3, 6). It is preserved in the Geological Institute at Münster.

Locality.-The type locality is Samos. None other is recorded.
Remarks.-This species is distinguished from all others by the number and character of the keels on the horn-cores. Although the proportions of the teeth vary in the two species, and although there are some differences in skull structure, it must not be overlooked that there is some probability that the present form may prove to be the male of Oioceros proaries Schlosser.

## Genus OVIS Linné.

## 1758. "Systema Naturae," Edit. X, p. 7o.

Diagnosis.-Ovicaprinae with lachrymal fossa of variable size ; no ethmoidal vacuity. Horn-cores broad anteriorly, triangular or much compressed, spiral.

Genotype.-Ovis aries Linné, 1758.
Remarks.-The early history of the true sheep is practically unknown, and the reference of the following species to this genus can only be regarded as provisional. Until the appearance of Andree's memoir in I926 Ovis was unknown from deposits older than the Pleistocene, and even in the Pleistocene it is rare. It is clear that Andree himself regards the generic identification as provisional. He says, "ich habe den vorliegenden Ovinen zur Gattung Ovis gestellt, da er meines Erachtens dieser näher steht als der Gattung Oioceros, die ja gänzlich andere Stirnzapfen und eine andere Ausbildung der Stirn aufweist."

## Ovis kuhlmanni Andree.

1926. Ovis kuhlmanni Andree, Palaeontographica, LXVII, Lief. 6, p. 172, pl. xiii, fig. 5, pl. xv, fig. II.

Diagnosis.--" Horn-cores very long, cross-section oval-elliptic, with a keel which begins externally on the side and probably makes a complete revolution round the horn which shows the same torsion, though not so markedly, as in Oioceros wegneri. The horn-cores are inserted very obliquely to the plane of the profile of the forehead and nasal bones. The greatest diameter [of the horn-cores] is at right angles to the [long] axis of the skull." (Andree, transl.)

Holotype. -The skull described and figured by Andree (1926, p. I72, pl. xiii, fig. 5, pl. xv, fig. II). It is preserved in the Geological Institute at Münster.

Locality.-The type locality is Samos. None other is recorded.
Remarks.-Andree points out certain features in the dentition on which he relies as a means of separating this species from Oioceros? proaries Schlosser. So far as one may judge from the cast, the shape and size of the bones of the face and braincase cannot be distinguished in the type-specimen.

## Specimen.

M 13165. Plaster cast of broken skull retaining the palate, and the lower part of the right horn-core. The original is the holotype (Andree, 1926, p. I72, pl. xiii, fig. 5, pl. xv, fig. II). Samos. (By exchange with the Geological Institute, Münster, 1926.)

## Subfamily $P S E U D O T R A G I N A E$.

Diagnosis.-" Skull moderately or strongly arched; lachrymal fossa large ; ethmoidal vacuity absent. Horns straight or curved, always inclined backward, elliptical or circular in cross-section. Cheek teeth brachyodont or moderately hypsodont, usually with weak basal pillar." (Schlosser, 1925.)

## Genus PROTORYX Major.

1891. C. R. Acad. Sci. Paris, CXIII, pp. 608-609.

Diagnosis.-Pseudotraginae of large size with high slender face, not expanded at the orbits, brain-case fairly long; face bent down on the basicranial axis almost to a right angle ; horn-cores almost upright or slightly tilted backward, more or less strongly curved, with a laterally compressed, elliptical cross-section, not keeled, considerably or only slightly divergent ; lachrymal fossa long and shallow ; supraorbital foramina not sunken in depressions; dentition moderately hypsodont, premolars rather shortened, weak basal pillars generally present in molars, ribs moderately developed.

Genotype.-The genotype is easily fixed. Major attributes to the genus an incomplete cranium from Pikermi figured and described, though not named, by Gaudry (1865, p. 289, pl. lii, fig. I) ; and a skull from Maragha in the British Museum (M 384I). As the only figured specimen the former is preferably to be selected for one of his species. Study of the material both in Lausanne and Paris, leaves very little doubt that Forsyth Major intended that Gaudry's Pikermi specimen should bear the name of Protoryx gaudryi, since it agrees very nearly with the Samos skulls preserved in Lausanne under that name, whereas an entirely different species is there named (in MS.) Protoryx carolinae. As it happens, however, Protoryx carolinae is the only species which he cites as occurring at Pikermi (I891, p. 608 ; 1892, p. 88 ; 1894, p. 4). We are therefore bound, whatever Major's intention may have been, to accept the name Protoryx carolinae for the Pikermi skull figured by Gaudry, and to abolish the name P. gaudryi. Schlosser's procedure has been similar, except that he was unaware of the characters of the specimens to which Major had affixed the manuscript name $P$. gaudryi.

Protoryx carolinae, as thus fixed, is here taken as the genotype.
Species and Nomenclature.-The genus Protoryx was founded by Forsyth Major in I891 for antelopes possessing curved, backwardly directed horns with an elliptical cross-section somewhat like those of Palaeoryx but more compressed laterally than in that genus, at any rate as it is represented by the species Palaeoryx pallasii.

He separated four species under the names $P$. carolinae, $P$. longiceps, $P$. gaudryi, and $P$. hippolyte. These were based on material collected in Samos, most of which is preserved in the Palaeontological Museum at Lausanne. Unfortunately neither figures nor descriptions exist to show on what details of structure Major relied for the separation of the four species. In his very diagnosis of the genus he made an unaccountable error in the sentence, "la région pariétale ne formant presque pas d'angle avec le chanfrein." Actually the face is bent down on the basicranial axis at very nearly a right angle in all the species.

Since Major left very little except the names which he gave to the skull figured by Gaudry and to the others collected by himself in Samos, it was exceedingly puzzling to decide how either the genus or any one of its four species should be defined. Schlosser (1904) solved the problem in the only way which was open to him, namely by largely disregarding Major's names as nomina mida. Unfortunately the material which he studied was exclusively that contained in the Munich Museum, and he does not appear to have seen the collections at Lausanne, Paris, or London. As the first necessity he emended Major's diagnosis of the genus Protoryx, calling special attention to the error indicated above. He definitely referred three skulls to the same species as the fragment figured by Gaudry, i.e. Protoryx carolinae, and compared with them two other skulls which he considered might represent either a variety or a sexual variant of the same. A second species, Protoryx hentscheli, was established on the dentition only. Finally, in founding the new genus Pseudotragus, with the one species Pseudotragus capricornis, for Protoryx-like antelopes with a much shortened cranium and expanded frontal, he suggested that his new species might include one or other of the forms separated by Major under the nomina nuda, Protoryx gaudryi and Protoryx hippolyte. It is shown later that the specimens preserved at Lausanne, to which Major fixed labels bearing the name Protoryx hippolyte, undoubtedly belong to the genus Pseudotragus. Since a specific separation of the Lausanne and Münich specimens seems to be inexpedient at present, we prefer to regard the former as a variety of Pseudotragus capricornis.

Of Major's names Protoryx longiceps alone remains to be considered. We have, below, adopted Major's name and described the species on the basis of a skull at Lausanne which was, we think, intended by Major to serve as his holotype. To P. longiceps we refer the skull from Samos figured by Schlosser (Igo4, pl. ix, fig. 8) as $P$. carolinae, since it is not conspecific with the holotype of the latter.

De Mecquenem (1925, p. 33, pl. iii, figs. 4, 5, pl. v, figs. 3, 4) described and figured a skull from Maragha. He accepted without question Schlosser's attribution of the Samos skull in Munich to the same species as the Pikermi skull in Paris, and being impressed by the similarity between the Maragha skull and that figured by Schlosser, he assigned to the former the name of $P$. carolinae. This is not correct.

Andree, like Schlosser, had seen neither the Paris type of Protoryx carolinae nor the collections in Lausanne and London, and has assumed that Schlosser correctly referred the Munich skull to Protoryx carolinae. He has distinguished three varieties of the species, (a) Schlosser's figured skull, in reality Protoryx longiceps n. sp. ex

Major MS., (b) Schlosser's Protoryx cf. carolinae, (c) Protoryx carolinae var. laticeps Andree. The two varieties last named are so similar to each other and to two wellpreserved skulls in Lausanne that it is impossible to separate them specifically. On the other hand, the two specimens described by Andree and the two in Lausanne display characters which are so markedly different from $P$. longiceps that, in our opinion, they must represent a distinct species to be known as Protoryx laticeps Andree. In the same memoir certain other skulls are referred to Protoryx hentscheli Schlosser, one to the type and another to a new variety tenuicornis. There is no skull either in Lausanne or in London which bears any close resemblance to this species. Andree has further established the new species Protoryx crassicornis; this appears to be specifically inseparable from the true $P$. carolinae Major, but on account of its absolutely smaller size, to judge by Andree's figure, and relatively stouter horns it may remain, for the present, as a variety of that species.

It is most unfortunate that such confusion in the nomenclature of the species of Protoryx should have arisen, but, for that reason, we have taken the utmost care in the examination both of the holotypes when available and of all other specimens to which we had access. This study of a larger number of specimens than was examined by any previous worker will, it is hoped, establish the nomenclature on a sounder and more durable basis.

Skull.-The horn-cores are placed over and slightly behind the orbits. They are laterally compressed, elliptical in cross-section, curved backwards without any torsion, divergent, and almost upright or only gently tilted backwards.

The brain-case is fairly long in comparison with the length of the face, which is bent down on the basicranial axis at an angle of approximately $90^{\circ}$. There appears to be some considerable amount of variation in the profile of the skull roof in the region where it joins the face. The frontal is bent: one part descends forwards to form the forehead and the other part forms the anterior portion of the roof of the skull. In a skull of Protoryx carolinae from Pikermi (M 10839) this change of direction is gentle and the profile is a regular curve. Schlosser ( 1904, p. 48) describes a skull which he refers to Protoryx cf. carolinae and of which he says, " here also the surfaces of the frontal form almost a right angle." A skull in the British Museum which is identified as Protoryx sp. displays this sharp change of direction, and here too the angle between the horizontal and descending portions of the frontal is approximately $90^{\circ}$. When the skull is held with the basicranial axis horizontal, the roof of the brain-case slopes downwards and backwards, and the occipital region is almost upright, or, it may be, slopes forward to a slight extent.

The orbits are comparatively small and the supra-orbital margin is not produced laterally to any great extent. The lachrymal fossa is long but shallow. The supraorbital foramina are small and not sunken in depressions.

Dentition.-The premolar series is short in comparison with the length of the molar series. All the molars have a basal pillar as a rule, but it is never very large except in the first molar.

It can be seen from various specimens of $P$. carolinae in the British Museum that the teeth are more hypsodont than they are in the different species of Tragocerus:
an observation also made by Schlosser on the Munich specimen of $P$. longiceps. Apart from this the dentition appears to be extraordinarily alike in the two genera, and, in the case of isolated sets of teeth separated from the skull, it is by no means clear that their identity can be firmly established. The various specimens in the British Museum differ somewhat in the ratio between the lengths of the premolar and molar series. In all of them, however, the premolars are relatively shorter than they are in Tragocerus amalthea. This is particularly noticeable in the case of $P^{2}$. The ratio is greatest in the case of $P$. carolinae and least in $P$. longiceps. Apart from its more slender premolars $P$. laticeps differs but little from $P$. carolinae in this respect. In $P$. carolinae the size of $P^{2}$ in comparison with the premolars behind it is worthy of note, and approaches Tragocerus. In $P$. longiceps $P^{2}$ is smaller than $P^{3}$. The internal wall of $P^{3}$ does not show the indented outline which is characteristic of Tragocerus amalthea, but such an outline is faintly indicated in $P^{2}$. The ribs on the external side of the upper molars are as strong as in Tragocerus, but not nearly so strong as they are in Palaeoryx pallasii.

## Protoryx carolinae Major.

(Pl. II, figs. $2,2 a$; Pl. III, figs. I, 3.)

1865. Antilope d'espèce indéterminée. Gaudry, "Anim. Foss. Attique," p. 289, pl. lii, fig. I.
1866. Protoryx carolinae Major, C. R. Acad. Sci. Paris, CXIII, pp. 6o8-60g.
1867. Protoryx gaudryi Major nom. mud., " Gisement Ossif. Mitylini," p. 28, no. 298; p. 30, no. 362.

Non Protoryx carolinae Major, I894, op. cit., p. 18, no. 28 ; p. 24, no. 201.
Nec Protoryx carolinae Schlosser, 1904, Beitr. Paläont. Geol. Oest.-Ung., XVII, p. 45, pl. ix, figs. I, 4, 8.
Nec Protoryx carolinae De Mecquenem, 1925, Ann. Paléont., XIV, p. 33, pl. iv, figs. 4, 5 ; pl. v, figs. 3, 4 .
Nec Protoryx carolinae Andree, I926, Palacontographica, LXVII, p. I5I, pl. xii, figs. 3, 3a, 4.
Diagnosis.-The largest species of Protoryx. It is characterized by the obtuse angle between the occipital and parietal surfaces of the brain-case; and by the greater posterior width of the horn-cores compared with the anterior width.

Holotype.-The skull from Pikermi described and figured by Gaudry (1865, p. 289, pl. lii, fig. r). It is preserved in the Natural History Museum at Paris.

Locality.--Pikermi is the type locality for this species which is also known from Samos.

Remarks.-This is the largest species of Protoryx known. The holotype of the species-the skull figured by Gaudry in 1865 -is imperfect and lacks the face and the teeth. This want is supplied by two skulls in the British Museum (M I839, MII4I5) collected by Sir Arthur Smith Woodward at Pikermi. These equal the Paris skull in most of their dimensions and show similar characters. Both of these are shown on Pl. III, figs. I, 3. In addition two imperfect skulls preserved in Lausanne (registered, 298, 362) under the name of Protoryx gaudryi agree well with the holotype. Both of them lack the teeth, and only one has the horn-cores preserved.

As in the other species of Protoryx, the cranial and facial axes are inclined to one another to such a degree as almost to form a right angle. The angle is slightly more
obtuse in $P$. longiceps and particularly in the specimen figured by Schlosser (1904, pl. ix, fig. 8) under the name $P$. carolinae. This specimen we regard as a variant of the typical $P$. longiceps.

The horn-cores have an elliptical cross-section. In contrast to $P$. longiceps, $P$. laticeps, and $P$. hentscheli, in which species the cross-section of the horn-cores is a regular ellipse, the cross-section in $P$. carolinae is wider behind than it is in front. The horn-cores slope backward at an extremely obtuse angle to the plane of the face, and for the first quarter of their length are straight ; they then curve rapidly backward until their tips are over the occipital condyles, if the basicranial axis be placed in a horizontal position. The amount of curvature is almost as great in $P$. longiceps, but in the Lausanne specimen of $P$. laticeps (registered number 201, under the name $P$. carolinae) the tips do not reach as far as the occipital condyles when the skull is held in a similar position. The divergence of the horns is moderately large, their tips being at least 150 mm . apart. This compares with 135 mm . in $P$. longiceps from Samos (Lausanne No. 22), 125 mm . in a skull of the same species from Maragha (M 384I B.M.G.D.), and II4 mm. in the skull figured by De Mecquenem ( 1925 , pl. v, fig. 3). On the other hand, the divergence of the horns is greater in $P$. laticeps (Lausanne Nos. 201, 28).

The orbits are circular, and are not situated very far in front of the horn-cores. The supra-orbital foramina are small and not sunken in depressions; shallow channels run forward from them towards the lachrymal. The lachrymal fossa is shallow but occupies a comparatively large area on the face ; beneath it the maxillae bulge somewhat above the teeth.

The width of the skull at the orbits much exceeds that in $P$. longiceps, as may be seen from the table on p. 42 , in which the measurements of the various species are compared. The breadth of the forehead of the holotype and of the skull No. 298 at Lausanne is the same and equals that of $P$. laticeps (Lausanne No. 20I). In the two British Museum skulls (M Io839, M II415) this dimension is greater than it is in the holotype, in correlation, no doubt, with the greater breadth of the horncores.

The absolute length of the cranium between the forehead and the occipital crest is actually no greater than it is in P. longiceps; it may even be less; but the slenderness of the cranium, which is a marked feature of the latter, sufficiently distinguishes it. P. laticeps, though almost as stoutly built as $P$. carolinae, is much shorter between the forehead and the occipital crest.

The one measurement in which $P$. carolinae distinctly exceeds all the other species is the width of the cranium at the auditory meatus. Another characteristic feature is the backward position of the occipital condyles which produces an obtuse angle between the occipital and parietal surfaces. This feature is present in all the skulls of $P$. carolinae, but less so in the British Museum M ro839 than in the others. On the other hand, P. laticeps, $P$. longiceps from Samos (Lausanne No. 22) and $P$. longiceps from Maragha (M 384I B.M.G.D.) do not show it.

In the Munich skull which we refer to $\stackrel{P}{P}$. longiceps the angle between the parietal and occipital surfaces is rather greater than in the other specimens of that species,
but in the other features which Schlosser mentions this skull undoubtedly conforms with $P$. longiceps.

Only in the two specimens in the British Museum is the upper dentition of the species definitely preserved with the remainder of the skull. Of these M II4I5 shows the dentition of the right-hand side, but the crown of $P^{2}$ has been lost; this is illustrated Pl. III, fig. 3. M Io839 retains $P^{3}$ and $M^{2-3}$ on the left-hand side. The length of the cheek teeth is considerably in excess of the corresponding measurement in P. longiceps as exemplified by the specimen described by de Mecquenem from Maragha, and by that from Samos described by Schlosser. To a less degree it is in excess of that of the maxilla (Lausanne No. 580) which forms part of skull No. 28 at Lausanne, which we refer to P. laticeps. The distortion of the two British Museum skulls does not permit the breadth of the palate to be accurately measured, but in the case of M 10839 it is over 47 mm . between the two last molars as compared with 45 mm . in the specimen of $P$. longiceps from Maragha described by de Mecquenem.

Two fairly complete mandibular rami (M I3066, M II497, B.M.G.D.) may be assigned to the present species. The first of these is figured on Pl. II, fig. 2. They belong to the right and left side respectively, but are not derived from the same individual. They agree very closely in structure with the corresponding rami of Tragocerus amalthea, but are distinguished by their greater dimensions and by the relative inferiority in size of $P_{2}$. The measurements of the smaller of the two are as follow:


In the Major collection from Samos is a large skull (M 4I98) which may be placed provisionally with Protoryx carolinae. It is complete in the frontal and facial region and has the two mandibular rami attached. The complete cheek-dentition is present on both sides, but in an advanced state of wear. The horn-cores are not well preserved. They are obviously elliptical in cross-section and laterally compressed. They therefore show their affinity to Protoryx rather than to Palaeoryx. It is not possible to be certain whether their cross-section is more like that of the horn-cores of Protoryx hentscheli or that found in Protoryx carolinae, but the absolute dimensions of the skull, the relatively larger space occupied by the premolars, the stronger ribs on the outer sides of the molars, and a faint re-entrant fold in the inner wall of $P^{2}$ seem to justify a provisional reference to $P$. carolinae. The large shallow lachrymal fossa is well shown, as are also the supra-orbital foramina which open on to the general level of the frontal, and which are not sunken in depressions. The atlas and axis vertebrae are still articulated with the occipital.

## List of Specimens.

Note.-Except M 4198 all these are from Pikermi, Woodward Colln.
M 4198. A skull, large and well-preserved. The horn-cores are damaged, the mandible is adherent, and the atlas and axis articulate with the occipital. Samos. Major Colln.
M ro839. A well-preserved skull with the horn-cores almost complete, basioccipital region somewhat deficient; face in front of the orbits rather crushed; $P^{3}$ and $M^{2-3}$ present on the left side, the whole of the right dentition broken away. Pl. III, figs. r, ra.
M II4I5. A skull somewhat distorted by pressure; left horn-core almost complete, right horn-core broken off 50 mm . above the base ; cheek dentition of the right side present with the exception of $P^{2}$ of which the roots only are preserved. Dentition figured Pl. III, fig. 3.
M II4r6. Palate with the complete cheek dentition from $P^{2}-M^{3}$ on either side. The premolars are quite unworn and above the crowns of $P^{3-4}$ are the remains of the milk dentition.
M II422. Left maxilla of a young individual with $d m^{4}$ and $M^{1}$ in an early stage of wear ; $M^{2}$ almost unworn.
M 53064. Left maxilla of a young individual with $d m^{3-4}$.
M 13065. Right maxilla with $P^{2-4}$.
M II 497. Left mandibular ramus with complete cheek dentition in a medium state of wear. The dimensions of this specimen exceed those of the following, and it is almost large enough to have belonged to the palate M II4r6.
M 13066. Right mandibular ramus with complete cheek dentition in a medium stage of wear. Pl. II, figs. 2, $2 a$.

## Protoryx carolinae var. crassicornis Andree.

1926. Protoryx crassicornis Andree, Palaeontographica, LXVII, p. 156, pl. xii, fig. I, pl. xiii, fig. 8.

Diagnosis.-Skull smaller; horn-cores with very large bases of elongate elliptical cross-section, tapering rapidly towards the tips, closely set together at the base.

Holotype.-The skull described and figured by Andree (1926, pl. xii, fig. I, pl. xiii, fig. 8). It is preserved in the Geological Institute at Münster.

Locality.-The type locality is Samos. None other is recorded.
Remarks.-The species Protoryx crassicornis Andree seems to agree very closely with P. carolinae Major in most of its characters. The shape of the cross-section of the horn-cores, their greater backward curvature, the comparative breadth of the cranium and the degree to which the face is bent down on the basicranial axis are features which it shares with $P$. carolinae, but with no other described species. The Münster skull appears to be of absolutely smaller dimensions; though the horncores are much larger and stand closer together at their base, the divergence is
similar. It does not seem feasible to regard these differences as more than varietal, so that we propose to designate the skull in question as Protoryx carolinae var. crassicornis Andree.

Protoryx longiceps n. sp. ex Major nom. nud.

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\text { (Pl. III, figs. } 2,2 a \text {; Pl. V, figs. 2, 2a.) }
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189r. Protoryx longiceps Major, nom. nud., C. R. Acad. Sci. Paris, CXIII, p. 608.
1894. Protoryx longiceps Major, nom. nud., "Gisement Ossif. Mitylini," p. 18, no. 22.
1904. Protoryx carolinae Schlosser, Beitr. Paläont. Geol. Oest.-Ung., XVII, p. 45, pl. ix, figs. I, 4, 8.
1925. Protoryx carolinae de Mecquenem, Ann. Paléont., XIV, p. 33, pl. iv, figs. 4, 5, pl. v, figs. 3, 4.
1926. Protoryx carolinae Andree, Palaeontographica, LXVII, p. 15I, pl. xii, figs. 3, 3 a, 4.

Diagnosis.-A Protoryx with the horn-cores set close together on the frontals. Horn-cores elliptical in cross-section, no wider posteriorly than anteriorly, more upright than in P. carolinae, divergence small, subparallel. Orbits directly beneath the horn-cores. Molars with a small basal pillar. Premolars without a re-entrant fold on the inner surface.

Holotype.-A skull in the Major collection at Lausanne. Catalogue number 22.
Paratype.-A skull from Maragha in the British Museum (M 384I). This is Major's geno-syntype of Protoryx (1891, p. 609).

Locality.-The type locality is Samos. The species is not known from any other European locality.

Remarks.-Both holotype and paratype are here figured for the first time. In both specimens the teeth are missing, but they are present in the skull from Maragha which was figured by De Mecquenem (1925) under the name Protoryx carolinae.

The angle between the basicranial and facial axes is rather more open than it is in $P$. carolinae, so that the face is less bent down on the brain-case.

The horn-cores are narrowly elliptical in cross-section and are no wider behind than in front. Their antero-posterior diameter is absolutely greater than it is in $P$. carolinae, and, having regard to their width and to the size of the skull, the difference between the two species is, in this respect, very marked. Compared with $P$. carolinae the horn-cores are rather more upright, and, although the backward curvature in the upper two-thirds is well-defined it is not so strong as in that species. As a consequence of this, the tips of the horn-cores hardly reach the vertical line from the occipital condyles. The most characteristic feature of the horns is their small divergence. This is trifling in the skull figured by Schlosser (I904) under the name $P$. carolinae; it is somewhat greater in the holotype, in the paratype, and in the skull from Maragha figured by De Mecquenem (1925), but is in any case noticeably less than in the species hitherto described. In this connection it may be well to mention that the association of the right horn-core with the remainder of the paratype is not absolutely proved, but, since it is the only horn-core of this size in the Maragha collection, and since it agrees perfectly in character and state of preservation with the left horn-core which is attached to the skull, it is considered exceedingly probable
that it belongs to the same individual. On this assumption the gap between this fragment and the base of the horn-core was filled with plaster. Thus the specimen as figured, though a partial restoration, represents, as nearly as may be, its original appearance.

The horn-cores stand very close together on the frontals, corresponding to the small width of the forehead at the orbits in three of the skulls known to us. The Münster skull figured by Andree ( 1926 , pl. xii, figs. 3, 4) agrees perfectly with the holotype and we have no doubt as to its specific identity. In the paratype the width at the orbit is much greater, but the horn-cores are also larger. Probably this skull is that of a male, and the other four those of females.

All five skulls of $P$. longiceps possess very slender crania. The length from the front margin of the horn-cores to the occipital crest is relatively great compared with the width of the occiput behind the fronto-parietal suture, or that at the auditory meatus. $P$. longiceps and $P$. carolinae are widely contrasted in this respect. $P$. laticeps is more brachycephalic than either of the other two species, but the difference between it and P. carolinae is not very marked. The holotype of $P$. longiceps does not show that backward position of the occipital condyles which is so pronounced in $P$. carolinae, and in the paratype the condyles are equally far forward, but the skull from Samos in the Munich collection seems to have a slightly greater tendency in the direction of $P$. carolinae.

The orbits are situated directly under the horn-cores. The supra-orbital foramina are small and not sunken.

The length of the premolar series as compared with the molar series is even less than it is in $P$. carolinae, the most striking difference being in the size of $P^{2}$ which is smaller than $P^{3}$, instead of being larger as it is in the Pikermi species. The teeth in the skull figured by De Mecquenem are in a moderately advanced stage of wear, and for this reason the height of the crowns cannot be ascertained with accuracy. Schlosser has, however, mentioned that the dentition is hypsodont. A small basal pillar is present in each of the molars ; the external ribs are not very strong. Neither molars nor premolars have any spurs of enamel projecting into the central cavity. None of the premolars has a re-entrant fold on the inner side.

Schlosser (1904, pl. ix, fig. 4) has figured a mandibular ramus which he considers to belong to his "P. carolinae" (i.e. P. longiceps) and de Mecquenem ( 1925 , pl. iv, fig. 4) has figured a ramus from Maragha which agrees almost exactly with it, and which he assigns to $P$. carolinae as identified by Schlosser. There are several isolated rami in Lausanne, some of them are slightly larger and some slightly smaller than that figured by De Mecquenem. The crowns of the teeth are more hypsodont than they are in Tragocerus amalthea, and although the basal pillars are not so well developed as they are in that species yet they are certainly present in $M_{1}$ and $M_{2}$ but are not so distinct in $M_{3}$. The premolar series is noticeably shorter than it is in $P$. carolinae, and still more so than in T. amalthea; $P_{2}$ is considerably smaller and simpler than $P_{3}$; in $P_{t}$ the valley on the internal side between the second and third wings is more open than it is in either $P$. carolinae or in Tragocerus amalthea. The lower dentition of $P$. longiceps is probably hard to distinguish from that of $P$. laticeps. In the Lausanne
collection there are possibly rami of both species, but I have no means of deciding to which of the two species they belong.

## Specimens.

The British Museum does not possess any specimens from European localities. The paratype (M384I) is from Ketschava, Maragha, Persia.

# Protoryx laticeps Andree. 

(Pl. IV, figs. I, $\mathrm{I} a, 2,3$.)

1894. Protoryx carolinae Major, "Gisement Ossif. Mitylini," p. 18, no. 28 ; p. 24, no. 201 ; p. 35, no. 580. 1904. Protoryx cf. carolinae Schlosser, Beitr. Paläont. Geol. Oest.-Ung., XVII, p. 48. 1926. Protoryx carolinae var. laticeps Andree, Palaeontographica, LXVII, Leif. 6, p. I53, pl. xii, figs. 5, 9.

Diagnosis.-A Protoryx "distinguished from Protoryx carolinae Maj. [i.e. $P$. longiceps, nov.] chiefly by the shorter and broader cranium. The horn-cores are longer and equally upright, their backward curvature, especially in the upper half, is, however, somewhat weaker than in carolinae [longiceps]. Moreover, the anterior margin of the orbit lies somewhat in front of the base of the horn-core, and the supra-orbital margin is noticeably more produced than in carolinae [longiceps]."

Holotype.-The skull described and figured by Andree (1926, p. I53, pl. xii, figs. 5, 9). It is preserved in the Geological Institute at Münster.

Locality.-The type locality is Samos. None other is recorded.
Remarks.-The skull figured by Andree lacks the dentition, but even apart from this it shows, as Andree has clearly stated, certain important differences from $P$. longiceps. These are its brachycephaly, its longer horn-cores, less curved than those of $P$. longiceps, and the somewhat more forward position of the orbits. In addition it is obvious that the divergence of the horn-cores is much greater than in either the Munich specimen of P. longiceps, or the holotype, or the paratype of that species. The cross-section of the horn-cores is not so elongate-elliptical as it is in P. longiceps. Even were there no other evidence available, we should be inclined to place a specific value on the differences mentioned.

As it happens, however, there are two skulls from Samos in the Lausanne collection (Cat. Nos. 28, 201) as well as a maxilla (Cat. No. 580 ) which is said to belong to skull No. 28, all of which have been labelled Protoryx carolinae. These three specimens are figured on Plate IV of the present catalogue. They represent one of the four species into which Major divided his genus Protoryx. Through some error he referred them to the same species as Gaudry's specimen from Pikermi.

The teeth of $P$. laticeps differ markedly from those of $P$. carolinae, and less so from those of $P$. hentscheli and $P$. longiceps. The skull is certainly distinct from that of $P$. carolinae, and, to a still greater degree, from those of $P$. hentscheli and $P$. longiceps. We therefore consider that the separation of this species from each of the three species named is justified.

So far as we are able to judge, without having seen the holotype, the only important differences between it and the skulls at Lausanne lie in its inferior size
and the slightly less degree of bending down of the face on the basicranial axis. The shape of the horn-cores of the two Lausanne specimens differs slightly in crosssection. One is somewhat more elongate, and the other somewhat less elongate than the cross-section of the horn-cores of the holotype.

We hesitate to consider the skulls at Lausanne as even varietally distinct from $P$. laticeps, since we are not certain that the holotype is not an immature individual. Moreover, we are unable to place in a different category the frontlet from Samos which Schlosser (1904, p. 48) described as Protoryx cf. carolinae. This skull, in respect of the breadth of the horn-core, is even farther removed from $P$. longiceps than either the Lausanne or Münster skulls. In addition to this, the horn-cores are rather more curved and do not bend outward as in the Lausanne skulls. These differences are no more than individual, and the four skulls are here united under the specific name Protoryx laticeps Andree.

The Lausanne skulls have the facial and basicranial axes inclined to each other at an angle of approximately $90^{\circ}$, a condition which is entirely unlike that obtaining in $P$. hentscheli. The breadth of the forehead at the orbits is greater than it is in the skulls which we refer to females of $P$. longiceps, but is approximately equal to that of the paratype of that species which we take to be a male. The orbits are circular and, like those of $P$. carolinae and $P$. longiceps, probably do not extend much further forward than the base of the horn-cores. The orbits of $P$. hentscheli differ in this respect. The supra-orbital foramina are small and not sunken in depressions.

The horn-cores, as in every other species of Protoryx are fairly upright and form an extremely obtuse angle with the plane of the face; they curve backward but not nearly so much as in the other three species of the genus, since their tips do not reach back as far as the occipital condyles when the basicranial axis is horizontal. Their degree of divergence is somewhat greater than it is in $P$. carolinae, and very considerably greater than it is in P. longiceps. They bend outward somewhat throughout their length, and their cross-section, though elongate and regularly elliptical, is much broader than it is in $P$. longiceps.

The length of the cranium relative to its breadth is markedly less than it is in $P$. longiceps, somewhat less than in $P$. carolinae, but probably much the same as in $P$. hentscheli. It is not easy to differentiate the species from either of the latter two by this character alone.

The occipital condyles are placed as in P. longiceps; they do not lie to the rear of the occipital crest as in P. carolinae.

As will be seen from the table on p. 42 , the united length of the premolar series in the Lausanne maxilla is distinctly greater relatively to that of the molar series than it is in the species $P$. longiceps, as exemplified by the specimen at Munich figured by Schlosser (1904, pl. ix, fig. 8) as P. carolinae, or in the species $P$. hentscheli. On the other hand, in $P$. carolinae the ratio is greater but the difference is trifling. $P^{2}$ in the Lausanne maxilla, and in a less degree the other premolars also, are, however, such extraordinarily slender teeth that there is no risk of mistaking them for the much broader ones of $P$. carolinae. Moreover, the molars of the latter species may be distinguished by the presence of median basal pillars.

The Lausanne dentition differs from that of $P$. hentscheli by the absence of shortening in $P^{2}$ or of distortion in $P^{4}$. The resemblances between them are as follow: (a) the ribs on the outer side of the upper molars are weak; (b) there is no trace of spurs of enamel projecting into the central cavities; (c) the inner wall of $P^{2}$ and $P^{3}$ shows no re-entrant fold in the enamel ; $(d)$ the median basal pillar is absent in $M^{1}$ and $M^{3}$ and only faintly present in $M^{2}$. The specimen of $P$. longiceps from Maragha described by De Mecquenem (1925, p. 33) as $P$. carolinae differs in $(a)$ and $(d)$ of the above, but, apart from these and the greater length of the premolars, the upper dentition of $P$. laticeps is more like this than any of the other species of Protoryx.

We cannot with certainty assign any mandible to this species, but it is possible that one might be found at Lausanne possessing characters different from those of $P$. longiceps to which species the majority must be referred.

## Protoryx hentscheli Schlosser.

1904. Protoryx hentscheli Schlosser, Beitr. Paläont. Geol. Oest.-Ung., p. 49, pl. ix, figs. 2, 3, 5-7.
1905. Protoryx hentscheli Andree, Palaeontographica, LXVII, pp. I54-155, pl. xii, fig. 2, pl. xiii, fig. 9.

Diagnosis.-A Protoryx with long horn-cores, broadly elliptical in cross-section, with a very weak anterior keel on their middle third and turning gently inwards in their upper third. Orbits large, oval, situated half in front of the base of the horncores; superior margin of the orbits greatly produced, in consequence of which the orbits are directed forwards to a greater extent than they are in the other species of Protoryx. Ribs and folds of the molar teeth much weaker than in P. longiceps; inner crescents rounded, not angular; postero-external angle of $M^{3}$ very large; third lobe of $M_{3}$ triangular ; enamel strongly wrinkled.

Syntypes.-A left maxilla, left mandibular ramus, an upper molar and premolar, all figured by Schlosser (1904, pl. ix, figs. 2, 3, 5, 6, 7). They are preserved in the Palaeontological Museum at Munich.

Locality.-The type locality is Samos. None other is recorded.
Remarks.-This species is distinguished from $P$. longiceps by its shorter, wider skull, and by the position of the orbits relative to the horn-cores. The latter feature also serves to separate it from P. laticeps. It differs from both species in the more primitive characters of the teeth.

## List of Specimens.

M I307I. Plaster cast of left mandibular ramus.
M 13072. Plaster cast of left maxilla.
M 13073. Plaster cast of upper premolar.
M 13074. Plaster cast of upper molar.
The originals of these four casts are the syntypes. Presented by the Munich Palaeontological Museum through Dr. G. E. Pilgrim, 1927.

Protoryx hentscheli var. tenuicornis Andree.
1926. Protoryx hentscheli var. temuicornis Andree, Palaeontographica, LXVII, p. 155, pl. xii, fig. 6, pl. xiii, fig. 2.
Diagnosis.-" The variations from the hentscheli type are the relatively somewhat broader and lower cranium, the sharper backward curvature of the horn-cores, and, especially, their more elongate elliptical cross-section at the base."

Holotype.---The skull figured by Andree (1926, pl. xii, fig. 6, pl. xiii, fig. 2). It is preserved in the Geological Institute at Münster.

Locality.-The type locality is Samos. None other is recorded.

## Genus PSEUDOTRAGUS Schlosser.

1904. Beitr. Paläont. Geol. Oest.-Ung., XVII, p. 51.

Diagnosis.-Antelopes of medium size with short face and cranium. Face bent down on the basi-cranial axis to less than a right angle. Forehead high and much expanded at the orbits. Lachrymal fossa deep, wide and high. Supraorbital foramina not sunken in depressions. Ethmoidal vacuity absent. Anterior margin of orbits over $M^{3}$. Horn-cores rather upright, only slightly curved, moderately divergent, with a narrowly or broadly elliptical, or sub-triangular crosssection, oblique to the antero-posterior axis of the skull. Dentition precociously hypsodont. Upper premolars stout, lower premolars slender.

Genotype.-Pseudotragus capricornis Schlosser (rgo4, p. 5I, pl. x, figs. y-8).
Species.-Apart from the genotype, and its variety described below, the only other species of this genus is $P$. longicornis Andree (1926, p. 147).

Remarks.-The members of this genus are distinguished from Protoryx by the short face and cranium, by the less degree of curvature of the horn-cores and their position relative to the orbits, by the large and deep lachrymal fossa, and by their more brachyodont teeth.

## Pseudotragus capricornis Schlosser.

1904. Psendotragus capricornis Schlosser, Beitr. Paläont. Geol. Oest.-Ung., XVII, pp. 51-56, pl. x, figs. I-8.
Diagnosis.-A Pseudotragus with horn-cores which are regularly elliptical in cross-section.

Lectotype.-The skull figured by Schlosser (1904, pl. x, figs. 7, $7 a, 7 b$ ) is hereby selected as the holotype of the species. It is preserved in the Palaeontological Museum at Munich.

Locality.-The type locality is Samos. None other is recorded.
Remarks.-A skull in the British Museum (M 4r93) shows many of the characters of the genus Pseudotragus as diagnosed by Schlosser. Such measurements as it is possible to obtain are given in the table on p. 42. Because of the loss of the hinder part of the brain-case those measurements which depend on the occipital crest and condyles are not given. It is, however, certain that, in proportion to the width at
the orbits, the brain-case must have been much shorter than in any species of Protoryx.

It is highly probable that the muzzle was short. The exceedingly overhanging orbital roof, the forward position of the orbits, the deep lachrymal fossa, the shape and position of the horn-cores, and the small supra-orbital foramina, which are not sunken in any way, all agree with the characters of P. capricornis. The horn-cores diverge regularly in this specimen, and do not appear to show the outward curve remarked in the skull at Lausanne which is discussed below.

The right third upper molar is the only tooth preserved in the skull. It is larger than the corresponding tooth in the holotype, having a length of 18 mm . compared with 15.5 mm . in the latter. On the other hand, the horn-cores of the British Museum specimen are smaller, and the width of the skull at the orbits is less than in the Munich type. The narrower forehead is probably correlated with the smaller horn-cores. There is at Munich another skull which agrees very closely with M 4193. Schlosser considers this specimen to represent the female and the holotype to represent the male of the species. If this be true it is very likely that the British Museum skull is that of a female.

It is just possible that the specimen should be referred to the following variety, supposing that variety to be sound, because it seems to have been a larger skull than the female in Munich, and the holotype of the variety, also a male, is larger than the holotype of the species.

## Specimen.

M 4193. A skull with the lower half of both horn-cores. It is badly broken, the occipital region, snout, and most of the teeth being lost. Samos. Forsyth Major Colln.

## Pseudotragus capricornis var. hippolyte nov. ex Major nom. nud.

1891. Protoryx hippolyte Major, nom. nud., C. R. Acad. Sci., Paris, CXIII, p. 608.
1892. Protoryx hippolyte Major, nom. nud., " Gisement Ossif. Mitylini," p. I8, no. 30.

Diagnosis.--Skull shorter, broader, and horn-cores more divergent than in the type. Horn-cores curved outward as well as backward.

Holotype.-A skull preserved at Lausanne. It bears the serial number 30 in the Major collection from Samos.

Locality.-The type locality is Samos. None other is recorded.
Remarks.--When defining his genus Protoryx Forsyth major wrote that the parietal region is " tantôt très allongée, tantôt plus courte." The second of these two variants was undoubtedly intended to include the Lausanne skull just described by me as Protoryx laticeps Andree as well as the skull catalogued as Protoryx hippolyte (Lausanne, No. 30). The former is unquestionably so close to the other species of Protoryx in all its characters that no one would separate it from that genus. As for the latter, Major might well have hesitated to assign it separate generic rank. Its characters are, (i) the shortness of the cranium from the forehead to the occipital
crest ; it appears from Schlosser's measurements that the Lausanne specimen is actually shorter than the Munich skull in this dimension; (ii) the strong expansion of the supra-orbital roof ; this is even more pronounced than in the holotype of the species, if one may judge by the width at the orbits, which is 144 mm . in the former and 130 mm . in the latter.

On account of the poor state of preservation of the Lausanne specimen, it is impossible to make any comparison between it and the skull preserved in Munich with regard to the following features mentioned by Schlosser as characteristic of P. capricornis: (i) thickening of the frontal suture, (ii) shortness of the muzzle, (iii) presence of a deep lachrymal fossa, (iv) position of the orbits, the front margin of which is over $M^{3}$, (v) more brachyodont teeth than in Protoryx, (vi) stoutness of the upper and slenderness of the lower premolars.

The horn-cores of the Lausanne skull are possibly shorter than in the holotype and the amount of divergence is certainly greater. Their backward curvature is less than in Protoryx longiceps and P. carolinae, but is about the same as in P. laticeps. The horns are curved not only backward but also outward, thus differing from those of two of the three species of Protoryx, and, apparently, also from those of the holotype of Pseudotragus capricornis. In all these the horns diverge rectilinearly from the base. In the Lausanne specimen of Protoryx laticeps there is also an outward bending of the horn-cores. Compared with Protoryx, the Lausanne specimen of P.capricornis has more slender horns. In this it differs greatly from Pseudotragus longicomis Andree, in which species, moreover, the cross-section of the horn-cores is markedly triangular. The lateral compression, as one gets above the base, is almost enough to produce an anterior keel. The long axis of the cross-section is set somewhat more obliquely to the antero-posterior axis of the skull than is the case in any of the species of Protoryx; for this reason when one faces the skull a large part of the external face of the horn-core can be seen but nothing of the inner face is visible. In all the species of Protoryx less of the outer and more of the inner side is visible from the same view point. The occipital condyles do not lie to the rear as they do in Protoryx carolinae, in consequence of this the parietal and occipital surfaces of the brain-case form a right angle.

To conclude. On account of the superiority in size of the Lausanne skull compared to the holotype of P. capricornis one might suppose it to be the male of the same species, were it not for the existence of the small skull described by Schlosser (I904, p. 53) and of the almost equally small skull in the British Museum described above. It is so probable that the two smaller skulls are those of females that one is inclined to assume that both the holotype and the Lausanne specimen are the skulls of males. Considering the differences between the Lausanne specimen and the two skulls preserved at Munich, namely, the difference in size, the width at the orbits, and the character of the horn-cores, we hesitate to assert that they are more than individual variations; at the same time it seems possible that the Lausanne skull may represent a definite race of the species $P$. capricornis and for this reason we have adopted the name originally given to it by Forsyth Major in manuscript.
COMPARATIVE MEASUREMENTS (IN MILLIMETRES) OF SPECIES OF PROTORYX AND PSEUDOTRAGUS.


## Pseudotragus longicornis Andree.

1926. Pseudotragus longicornis Andree, Palaeontographica, LXVII, p. 147, pl. x, figs. 2, 3.

Diagnosis.-A Pseudotragus with horn-cores of triangular cross-section.
Holotype.-The skull figured by Andree (1926, p. x, figs. 2, 3). It is preserved in the State Museum of Natural History at Vienna, registered number V. 37.

Locality.-The type locality is Samos. None other is recorded.
Remarks.-Andree regards this species as forming a connecting link between the genera Pseudotragus and Protoryx. He points out that it agrees with Pseudotragus in the characters of the skull as a whole, the short cranium and snout, the large and deep lachrymal fossa. The characters of the supraorbital foramina are the same in the two species, and they also agree in the amount of curvature of the horn-cores. Characters which it shares with the form he terms Protoryx carolinae (i.e. P. longiceps Pilgr. \& Hopw.) are the longer and more divergent horn-cores, the less degree of thickening of the frontal and fronto-parietal sutures, and the shape of the fronto-nasal suture which is that of an inverted V instead of being M-shaped as it is in Pseudotragus. The teeth are scarcely separable from those of P. capricornis.

## Genus PACHYTRAGUS Schlosser.

## 1904. Beitr. Paläont. Geol. Oest.-Ung., XVII, p. 56.

DiAgnosis.-"Antelopes of medium size with a short face; forehead rapidly rising, somewhat concave, with wide supra-orbital foramina ; cranium sloping steeply [away from the face]; cranial sutures greatly thickened; orbits somewhat in front of the bases of the horn-cores and greatly produced laterally; long but shallow lachrymal fossae ; relatively long, stout horn-cores, strongly divergent, curving gently outward and backward, rounded triangular in cross-section, with a more or less strong anterior keel, and, on the posterior surface, longitudinal furrows. The premolars are of considerable size and, in the lower jaw, of complicated structure ; the lower molars are fairly hypsodont, the upper ones broad with deep wide valleys."

Genotype.-Pachytragus crassicornis Schlosser.
Remarks.-This genus is not represented in the British Museum collections. The generic diagnosis quoted is that given by Schlosser ; as Andree points out (I926, p. I49) it needs some slight amendment. The chief alteration is, "with, or without, an anterior keel and furrows on the posterior surface of the horn-core."

## Pachytragus crassicornis Schlosser.

1904. Pachytragus crassicornis Schlosser, Beitr. Paläont. Geol. Oest.-Ung., XVII, p. 54, pl. xi, figs. X-5, It.

Diagnosis.-A Pachytragus with an anterior keel to the horn-cores; the orbits much produced laterally ; supra-orbital foramina large.

Lectotype.-The specimen figured by Schlosser (1904, pl. xi, fig. IIa) is hereby taken as the holotype of the species. It is preserved in the Palaeontological Museum at Munich.

Locality.-Samos is the type and only known locality.
Remarks.-It is quite uncertain whether the teeth ascribed by Schlosser to this species are correctly identified. The dentitions which he examined did not belong to any of the skull fragments bearing horn-cores. More suitable material is needed before this point can be decided.

## Pachytragus schlosseri Andree.

1926. Pachytragus schlosseri Andree, Palaeontographica, LXVII, p. 148, pl. xii, fig. 7; pl. xiii, fig. 3 ; pl. xiv, fig. 4.
Diagnosis.-A Pachytragus which differs from the genotype in the orbits, which are situated further forward, and are not so produced laterally; in the supra-orbital foramina, which are small ; and in the horn-cores, which have only a slight suggestion of an anterior keel, and which may or may not have longitudinal furrows posteriorly.

Lectotype.--The skull and horn-cores figured by Andree (1926, pl. xiii, fig. 3, pl. xiv, fig. 4). It is preserved in the State Museum of Natural History at Vienna, registered number II, 2.

Locality.-Samos is the type and only known locality.
Remarks.-The teeth are, in general, very like those ascribed to $P$. crassicornis by Schlosser, and it is not certain whether the teeth which he examined may not prove to belong to the present species.

## Genus TRAGOCERUS Gaudry.

1861. C. R. Acad. Sci. Paris, LII, p. 298.

Diagnosis.-Antelopes of medium or fairly large size. Skull long and slender ; face very slightly bent down on the basicranial axis; horns long to moderately short, tilted backwards, slightly curved, occasionally very faintly twisted, more or less divergent, strongly compressed laterally with a strong anterior keel, generally close together in front and separated behind, often connected by a high frontal swelling from which the contour falls away to the front and to the rear ; lachrymal fossa variable but generally long and rather deep; supra-orbital foramina not sunken in depressions. Dentition moderately hypsodont; premolar series large and long ; $P_{2}$ with a rather complex structure; molars with basal pillars and moderately strong ribs.

Genotype.-Capra amalthea Roth \& Wagner (1854, p. 453, pl. xii, fig. 2).
Species.-In addition to the genotype, several other species of Tragocerus have been described from material found both in Europe and in Asia, but most of them are not represented in the British Museum collections. Short accounts of the European forms not represented are given below : they are T. rugosifrons Schlosser (1904), T. frolovi Pavlow (I9I3), T. validus Khomenko (I913), T. leskervitschi Borissiak (1914), T. curvicornis Andree (1926), and T. recticornis Andree (1926).

The form usually known as Tragocerus valenciennesi Gaudry (1865) does not
present the characters common to the above-mentioned species. We have, therefore, separated it as a distinct genus, Graecoryx (infra).

Skull.-The horn-cores are peculiarly goat-like. They are placed obliquely in relation to the sagittal plane of the skull, and are strongly compressed from either side. The anterior edge forms a strong, sharp keel which starts in an antero-internal position at the base of the horn-core and passes gently outwards as it is traced towards the apex. A second keel, equally distinct, though not so sharp, passes directly upwards from the postero-external angle of the horn-core. In the extent to which they are separated at the base, and in the angle at which they diverge, the horncores show considerable variation, not only as between species, but also as between races and individuals of the same species.

The cranium is comparatively long in relation to the face, which is bent down on the basicranial axis to a relatively slight extent. If the skull be posed so that this axis is horizontal the roof of the brain-case, seen from the side, is also horizontal, or very nearly so. The occipital is then practically perpendicular, and the supraoccipital overhangs it to a small amount. Strong crests for the temporal muscles are a marked feature of the parietals in the majority of skulls. The frontals, where they give rise to the horn-cores, are elevated into a boss which varies considerably in size in different species and individuals.

Although the facial part of the skull is usually much crushed the main features are fairly well known. The orbits are large with projecting rims. They face outwards, and but very slightly forwards. Their posterior margin passes up into the hinder surface of the horn-core with hardly any interruption. As a rule the lachrymal fossa is long and fairly deep. Its upper end is situate about half to three-quarters of the way up the inner margin of the orbit. The lower end appears to vary in position from a point above $M^{1}$ to a point considerably in advance of this above $P^{2}$ or $P^{3}$. The supra-orbital foramina are small and are not sunken in depressions. The nasal bones are small and pointed at their upper ends.

Dentition.-Lack of material prevents a general account. The dentition of T. amalthea, however, is described in some detail (infra).

## Tragocerus amalthea Roth \& Wagner.

1854. Antilope speciosa Roth \& Wagner, Abh. Bayer. Akad. Wiss., VII, p. 452, pl. xiv (viii), fig. I.
1855. Capra amalthea Roth \& Wagner, op. cit., p. 453, pl. xii (vi), fig. 2.
1856. Antilope arcuata Gervais, "Zool. Paléont. Franç.," ed. 2, p. I4o.
1857. Tragocerus amaltheus Gaudry, "Anim. Foss. Attique," p. 278, pls. xlviii-li.

Diagnosis-A Tragocerus in which the angle between the forehead and the roof of the brain-case is approximately $120^{\circ}$. Orbits entirely underneath the bases of the horn-cores. Horn-cores nearly straight, long, with a sharp anterior keel, which, seen from the front, is slightly curved outwards. Horn-cores diverging at an angle of approximately $38^{\circ}$; closely approximated at the base.

Holotype.-The horn-core figured by Roth and Wagner (op. cit., pl. xii (vi), fig. 2). It is preserved in the Palaeontological Museum at Munich.

Nomenclature.-As was pointed out by Gaudry (1865, p. 279), there is every
probability that the palate described and figured by Roth and Wagner (I854, p. 452, pl. xiv (viii), fig. I) belongs to this species. Both names are equally available, but, since the difference between them is one of page-priority only, and since amalthea is the name used hitherto, there does not appear to be any real reason for making a change.

The form in which the trivial name is generally written, amaltheus, is wrong. Amalthea, being a substantive, does not change its ending with the gender of the generic name.

Localities.-The type-locality is Pikermi. The species is also known from Samos and Mont Léberon.

Other European localities are as follow: France, Coirons, Ardèche (Depéret, 1887, p. 245) ; Croix-Rousse, Lyons (Depéret, loc. cit.) ; Montredon, near Bize, Aude (Depéret, I895, p. 433) ; Puy-Courny, Cantal (Boule, 1896, p. 222). Hungary, Baltavár, Komitat Vas (Pethö, 1884, p. 68) ; ?Polgárdi, Komitat Fejér (Kormos, 19II, p. 187). Macedonia, Veles (Schlosser, 192I, p. 38). Portugal, Archino, near Ota (Roman, 1907, p. 70). Rumania, Taraklia, Bendery (Khomenko, I913, p. 123). Spain, Concud (Cortázar, 1885, p. 187).

Remarks.-Gaudry (1873, p. 55) distinguished three "races" of this species, to which Schlosser (1904, p. 59) added the variety parvidens, and Andree (1926, p. I4I) two more " races."

In dealing with so variable a species it becomes a matter of importance to determine which is the functional type. The species was originally described from an isolated horn-core found at Pikermi so that the functional type must be one of the " races " from that locality. Of the three described by Gaudry the first is the common one, and it agrees very well with the description of the holotype given by Roth and Wagner. For these reasons, then, Gaudry's first " race " is taken as the functional type of the species Tragocerus amalthea.

It is doubtful whether it would not be more advantageous to separate the variants as distinct species. Taking into consideration, however, the fragmentary nature of much of the material, there is no doubt that it is more convenient to keep them all under the one name for the present ; fully realising that such a course is provisional only, and that future work may make it essential that these varieties should be elevated to specific rank.

## I. "Race à cornes divergentes."

1873. Gaudry, "Anim. Foss. Léberon," p. 55, pl. x, fig. 2.

This is the functional type of the species. It is characterized by long, divergent horn-cores, which are not relatively very broad, and which are close together at the base.

All the frontlets in the British Museum belong to this group. In some of them, however, the horns are less closely approximated, and the frontal swelling on which they stand is not very prominent. The strength of the latter feature varies by
gentle transition from a very faint swelling, which does not make any sudden change in the profile, to a most pronounced ridge which falls suddenly in front and has a deep depression behind it. The horn-cores of M 12987 are situated rather obliquely on the frontal, but their divergence is as in the other specimens. The dimensions of the horn-cores vary in their actual length, and in their relative sagittal and transverse diameters. In many there is a decided tendency to twist, whereas in others the anterior ridge lies quite evenly in the same plane without any trace of torsion.

Nothing is known of the variation of the teeth among the various "races." On this account the dentition is dealt with here as though every specimen in the collection were definitely referable to the first race.

As Schlosser has observed, the dentition is decidedly hypsodont, though not so much as in many recent antelopes. It differs in this from Graecoryx valenciennesi, as well as in the smaller relative length of the premolar series. The premolars are broad; $P^{3}$ is generally, though not invariably, the broadest, especially in its posterior half. $P^{4}$ is sometimes as broad or broader than $P^{3}$. The inner wall of both $P^{3}$ and $P^{4}$ is more or less indented; this is not the case in Protoryx carolinae. Moreover, the premolar series, especially $P^{2}$, is longer, and the tooth crowns are less high than in that species. The resemblance between the dentitions of the two species is, however, extraordinarily close.

The structure of the lower teeth is remarkably uniform, although the absolute dimensions vary. Still more do the different specimens vary in the depth of the ramus. Thus, in M II456, with a length of 115 mm . for the cheek-teeth series, the depth of the ramus internally below $M_{2}$ is only 29 mm ., whereas in MII455, with a corresponding length of $I I 4 \mathrm{~mm}$. for the cheek-teeth series, the depth of the ramus below $M_{2}$ is 37 mm .

There are some twenty mandibular rami in the Woodward collection which agree with T. amalthea in the general structure of the teeth. They differ from it only in their absolutely inferior size, and also in the greater proportionate length of the premolar series and of the front part of the jaw. In M. I3068a, which is typical of them all, the length of the entire series of cheek-teeth is 98 mm . This is actually slightly in excess of the corresponding dimension of the smallest member of the series referred to T. amalthea by Gaudry (1865, p. 284). The length of the premolar series in M I3068a is, however, 44 mm ., whereas in the small Paris specimen quoted above it is only 40 mm . The distance between the alveolus of $P_{2}$ and the dental foramen is 30 mm ., which is the same as in a British Museum specimen of $T$. amalthea ( M II456) in which the length of the cheek-teeth series is II4 mm. In most of the rami referred to, the depth of the ramus internally below $M_{2}$ is about 29 mm . These rami are too large for Graecoryx valenciennesi, in which species, moreover, the premolar series is even longer.

The specimens may be placed provisionally in Tragocerus amalthea, failing any evidence of another species to which they may reasonably be referred.

## II. "Race à cornes rapprochées."

1873. Gaudry, op. cit., p. 55, pl. x, fig. r.
" The second race is characterized by its horns which are shorter, broader, usually not so thick, approximated to each other, and placed very obliquely on the frontals, so that if the planes were produced they would meet at a less acute angle " [than in the first race]. (Gaudry, transl.)

## III. "Race à cornes écartées."

1873. Gaudry, op. cit., p. 55, pl. x, fig. 3 .
" The third race is characterized by its horn-cores, which are relatively small, narrow, slightly divergent, and widely separate at the base." (Gaudry, transl.)

> IV. " Vierte Rasse, var. nov."
1926. Andree, Palaeontographica, LXVII, 141, pl. x, figs. 4, 6 .
" The most characteristic feature as compared with the first three races and $T$. parvidens consists in the strong curvature of the keel (seen from the front), which is much weaker in the first race, is lacking in the second and third, and is unknown in parvidens. Further, there is behind the horn-cores a large but shallow depression, which is surrounded on all sides by a swelling. This depression is small in the second and third races, and in parvidens, and only in the third has it a slight margin.
" The following special characters distinguish the fourth race from the others:
"The axis of the skull is less bent than it is in the first variety ( $\mathrm{I} 25^{\circ}$ as against I20 ${ }^{\circ}$ ). In profile the horn-cores display the undulating curve hitherto peculiar to the second race. The curvature of the hinder profile of the horn-cores is slight. Furthermore, the anterior margin of the orbits is somewhat in advance of the bases of the horn-cores.
"The horn-cores are distinctly longer than they are in the second race, and the anterior margins of their bases are not so extended on the forehead.
" The third race lacks the curved keel on the horn-cores and their curved profile which are found in the fourth. The horn-cores are, on the whole, decidedly smaller.
" From parvidens the fourth race is further distinguished by the absence of a second posterior keel, and a depression in front of the horn-cores. The bend in the axis of the skull is greater ( $\mathrm{I} 25^{\circ}$ to $140^{\circ}$ )." (Andree, transl.)
V. "Fünfte Rasse, var. nov."
1926. Andree, op. cit., p. 14I, pl. x, figs. 5, 8.
" The fifth race is characterized by the very oblique position of the horns. Their upper ends are bent inwards, and the anterior keels (seen from the front) are more strongly curved than is the case in the fourth variety. The depression behind the horns is relatively deep and completely surrounded by a thick swelling-thus
this feature is much more pronounced than in the fourth race-and the bend in the axis of the skull is as slight as in parvidens Schl. ( $145^{\circ}$ ). As in the third race, and in parvidens, half of the orbit lies in front of the base of the horn-core. The undulating profile of the keel is present."

## Tragocerus amalthea var. parvidens Schlosser.

1904. Schlosser, Beitr. Paläont. Geol. Oest.-Ung., XVII, p. 59, pl. xi, figs. 6-9, pl. xii, fig. $5 \cdot$

Diagnosis.-Cheek-teeth relatively smaller than in the functional type ; horncores with two posterior keels ; a depression in front of the horn-cores.

Lectotype.-The imperfect cranium figured by Schlosser (op. cit., pl. xii, fig. 5) is hereby taken as the holotype of this variety. It is preserved in the Palaeontological Museum at Munich.

Locality.-Samos. The only other locality in Europe is Taraklia, Bendery, Rumania (Khomenko, 1913, p. 123).

Remarks.-A badly preserved skull from Samos (M 4196) seems referable to this variety. It is rather smaller than the holotype, but agrees with it in the relative proportions of the teeth and horn-cores. The latter, though much broken, have the narrow elliptical section of Tragocerus amalthea, with a sharp keel in front and broadening considerably behind. Their sagittal diameter is 45 mm . and their maximum transverse diameter 3 I mm . They are 13 mm . apart at their anterior end and have no connecting ridge. The combined length of $M^{2-3}$, the only teeth preserved, is 38 mm . These two teeth are much worn but they display the general aspect of Tragocerus and have marked basal pillars.

Another frontlet (M 4194) has the horn-cores better preserved. The left horncore, which is preserved for a distance of $\mathbf{1 0 3} \mathrm{mm}$., affords some evidence that the anterior keel was only slightly swept outwards.

A third specimen ( $\mathrm{M}_{4}$ 2I4) shows the right horn-core attached to a portion of the frontal. The horn-core is broken but must have been short. It is somewhat curved. The sagittal diameter is 54 mm . and the transverse diameter 28 mm .

A right maxilla with $\mathrm{M}^{2}$, and $\mathrm{M}^{3}$ almost unworn, seems to resemble Tragocerus. The teeth agree in size with those in skull M 4196 .

Andree regards this form as a species distinct from T. amalthea. As remarked above we have open minds on the point.

## List of Specimens.

## i. Tragocerus amalthea.

Except when otherwise stated, these belong to the Woodward collection from Pikermi.

M 10835. Skull almost complete in the frontal and occipital regions; basicranial region somewhat broken ; face broken in nasal region ; cheekdentition (in an advanced stage of wear) perfect on the right side,
broken on the left ; horn-cores long and narrow ; pronounced frontal ridge.
M ro836. Skull showing occipital and frontal regions well ; with well-preserved horn-cores ; face imperfect, showing only right side with two broken molars.
M 10837. Skull showing frontal and occipital regions; with well-preserved horn-cores ; face and teeth wanting.
M II420. Skull moderately complete; occipital condyles broken off and basicranial region battered; horn-cores much more divergent than in the other specimens; cheek-dentition in place, but teeth worn and battered.
M II425. Skull with right horn-core only preserved; pronounced ridge between the horn-cores ; laterally crushed but showing the complete dentition in an early stage of wear with the exception of the right $P^{2}$.
M 4069. Horn-core. Pikermi. By exchange 1889.
M 5429. Frontlet with long, narrow, slightly twisted horn-cores. Pikermi. Purchased 1894.
M ro838. Frontlet with short, divergent horn-cores.
MII423. Three frontlets with short, divergent horn-cores, rather far apart at the base, and with little or no frontal swelling.
M II429. Single horn-core of left side attached to parietal region of the skull; long and narrow, without any twist.
MII48I. Isolated horn-core very similar to that of the preceding.
M 12987. Frontlet with slender horn-cores somewhat crushed, but apparently with their sagittal diameter lying rather obliquely to the anteriorposterior axis of the skull.
36597. Fragmentary palate with $P^{2}$ of either side. Pinermi. Presd. by P. J. Gran, Esq., 1853 .

MII424. Palate of a young individual containing the three molars and the three milk-molars on either side. Premolars partly exposed as germ.
MII427. Palate of a mature individual showing the complete cheek-dentition in a fairly advanced stage of wear.
49706. Left maxilla with $P^{2}-M^{3}$. Pikermi. Purchased 1879.
49707. Right maxilla of a young individual with $d m^{2}-d m^{4}$ and $M^{1}$. Pikerimi. Purchased 1879.
M II42I. Right maxilla with complete series of cheek-teeth in an intermediate stage of wear ; $P^{3}$ exceptionally broad posteriorly.
MII454. Immature right maxilla with $d m^{3}$ and $d m^{4}$ little worn, and $M^{1}$ quite unworn.
M II459. Immature right maxilla with the broken $d m^{4}$ and $M^{3}$ just being cut.
M 12976. Portion of left maxilla with three premolars; $P^{1}$ remarkable by having the fold in the external wall median, instead of in the anterior half of the tooth
M 12977. Portion of left maxilla with three premolars.

M 12978. Right maxilla with three molars; $M^{3}$ in a very early stage of wear.
M 12979. Right maxilla with the cheek teeth, except $P^{2}$, in a rather early stage of wear ; $P^{3}$ both shorter and narrower than in the preceding specimen.
M 12981. Right maxilla with the cheek-dentition, except $P^{2}, P^{3}$ broad posteriorly ; belonging to a distinctly smaller individual than either Mil42I or Mr2979.
49708. Left mandibular ramus lacking $P_{2}$. Pikermi. Purchased 1879.
49709. An incomplete mandibular ramus of a young individual with $d m_{3}-d m_{4}$ and $M_{1}$. Pikermi. Purchased 1879 .
4972I. An incomplete right mandibular ramus with $M_{1}$ and $M_{2}$. Mont Léberon. Purchased 1879 .
M II455. Left mandibular ramus; $P_{2}$ is a little shorter and stouter than usual, and the external wall of $P_{4}$ has a marked median tubercle.
MII456. Left mandibular ramus, complete with the dentition from the incisor alveoli to $M_{3}$.
M II498. Two left mandibular rami (one incomplete) of young individuals of the same type as the preceding ; $d m_{4}$ in place, $P_{3}$ just cut, $P_{2}$ just about to cut the gum, and $M_{3}$ unworn.
MII502. Two right mandibular rami, slightly stouter and deeper than the specimen M II456, though the teeth are of equal size.
M 1297I. Left mandibular ramus belonging to larger individuals than either MII455 or MiI456. The premolars are relatively larger than in those specimens.
M 12972. Two right mandibular rami of young individuals showing $d m_{2-4}$ in place and $M_{1-2}$ in an early stage of wear.
M 12973. Right and left mandibular rami of a young individual with $d m_{2-4}$ in place, $M_{1-2}$ almost unworn and $M_{3}$ uncut.
M 12974. Incomplete left mandibular ramus showing the abnormality of a supranumerary molar.
M r 2980. Right and left mandibular rami.
M r3068. Twenty mandibular rami.
49710-II. Right astragalus, distal end of a metapodial and three phalanges. Pikermi. Purchased 1879.
Note.-In the following specimens the depth of the ramus considerably exceeds that of the preceding specimens, and it is just possible that they may belong to small individuals of Protoryx carolinae.
M 5430. Right and left mandibular rami with alveolus of $P_{2}$ and retaining $P_{3}-M_{3}$. Pikermi. Purchased 1894.
Mri455a. Right mandibular ramus with $P_{2}-M_{3}$.
M Ir 507. Right mandibular ramus with $P_{3}-M_{3}$.

## ii. T. amalthea parvidens.

All these are in the Major collection from Samos.
M 4194. Frontlet with both horn-cores broken.
M 4I96. Skull, crushed and broken.
M 42I4. Frontlet with right horn-core (broken).
M I3025. Right maxilla with $M^{2-3}$.

## Tragocerus curvicornis Andree.

1926. Tragocerus curvicornis Andree, Palaeontographica, LXVII, p. 142, pl. xi, figs. 6-7.

Diagnosis.-A Tragocerus in which the horn-cores are strongly curved backwards.
Holotype. -The brain-case and horn-cores described and figured by Andree (op. cit., pl. xi, figs. 6-7). The specimen is preserved in the Geological Institute at Münster.

Locality.-The type locality is Samos. None other is recorded.
Remarks.-This species is much larger than $T$. amalthea. It is remarkable for the strong backward curvature of the horns.

## Tragocerus frolovi Pavlow.

1913. Tragocerus frolovi Marie Pavlow, Nouv. Mém. Soc. Nat. Moscou, XVII, p. 8, pl. i, fig. 5.

Diagnosis.-A Tragocerus in which the horn-cores are placed above and partly in front of the orbits, and pass obliquely backwards ; anterior keels passing obliquely upwards and outwards, merging at the base into a rugosity below the horn-cores.

Holotype.-The skull figured by Pavlow (op. cit., pl. i, fig. 5). It is preserved in the Geological Cabinet of the University of Moscow.

Locality.-The type locality is Tchobroutchi, Bessarabia. None other is recorded.

Remarks.-This form appears to be very close to T. rugosifrons Schlosser, if, indeed, it is not actually conspecific.

## Tragocerus leskewitschi Borissiak.

1914. Tragocerus leskewitschi Borissiak, Mém. Com. Géol. St. Peter., N.S., livr. 87, pp. 36, 127, pl. iv.

Diagnosis.-A Tragocerus of small size with short horns (? 170 mm .) ; horncores disposed as in the type of $T$. amalthea, and with a single keel back and front ; angle between facial and basicranial axes slight ; upper premolar series relatively short ; structure of $P^{3}$ nearer to that of $P^{4}$ than it is to that of $P^{2}$.

Lectotype.-The skull figured by Borissiak (op. cit., pl. iv, figs. $1 a-\mathrm{I} c$ ) is hereby chosen as the type of the species.

It does not appear from the French summary where the specimen is preserved.
Locality.-The type locality is Sebastopol. None other is recorded.
Remarks.-This species is said to have been found in a pre-Pontian deposit, namely the upper part of the middle Sarmatian ; it is included here for the sake of completeness.

## Tragocerus recticornis Andree.

1926. Tragocerus recticornis Andree, Palaeontographica, LXVII, p. 143, pl. xi, figs. 5, 9.

Diagnosis.-A Tragocerus with long horns (370-390? mm.) ; one keel ; horncores almost straight, set very obliquely on the frontal.

Holotype.-The skull figured by Andree (op. cit., pl. xi, figs. 5, 9). It is preserved in the Natural History Museum at Stuttgart ; regd. number 13269.

Locality.-The type locality is Samos. None other is recorded.
Remarks.-This species is close to T. rugosifrons Schlosser.

## Tragocerus rugosifrons Schlosser.

1904. Tragocerus rugosifrons Schlosser, Beitr. Paläont. Geol. Oest.-Ung., XVII, p. 64, pl. xii (ix), figs. I-4, 6.

Diagnosis.-A Tragocerus with a strongly marked semi-circular elevation in the centre of the forehead into which the bases of the horn-cores pass. Elevation and forehead rough and granulate.

Lectotype.-The skull described and figured by Scholsser (op. cit., pl. xii, fig. 6) is hereby chosen as the holotype of the species.

Locality.-The type locality is Samos. The species is also known from Rumania, Taraklia, Bendery (Khomenko, I9I3, p. I23).

Remarks.-The premolars are relatively smaller than those of $T$. amalthea. Furthermore, the enamel on the outer surface of the upper molars is more strongly folded, and the basal columns are more strongly developed.

This species differs from T. amalthea in the structure of the skull which is conspicuously larger, and with wider frontals, which are deeply excavate behind the horns. The lachrymal fossae are very large and deep; the hinder half is formed solely by the lachrymal. More than half the orbit is in front of the horn-core ; its anterior margin is over the last molar.

The horn-cores are elongate-triangular in cross-section, with one keel in front, and with the hinder face rounded. They are rather more divergent than in T. amalthea, and more strongly inclined backwards, but in most other respects the horn-cores of the two species are similar.

## Tragocerus validus Khomenko.

1913. Tragocerus validus Khomenko, Annu. Géol. Min. Russie, XV, p. 124, pl. viii, fig. I2.

Holotype.-The three teeth figured by Khomenko (op. cit., pl. viii, fig. 2).
They are preserved at Odessa.
Locality.-The type locality is Taraklia, Bendery, Rumania.
Remarks.-This species is described in Russian and only appears as a name in the French summary. Khomenko gives the following comparison with T. amalthea :-


The figure is poor and the species is unsatisfactory.

## Genus GRAECORYX nov.

1865. Tragocerus Gaudry, pars, "Anim. Foss. Attique," p. 288.

Diagnosis.-Antelopes of moderately large size, with narrow elongate muzzle, and broad frontals ; face slightly bent down on basicranial axis ; lachrymal fossa large but shallow ; supra-orbital foramina small, not sunken ; horn-cores straight, small, tilted backward, with an elliptical cross-section, narrower anteriorly but not keeled, standing far apart. Dentition with retarded hypsodonty; premolar series exceptionally long, especially the front premolars ; ribs of upper molars fairly strong, basal pillars present, without spurs of enamel projecting into the central cavity.

Genotype.-Tragocerus valenciennesi Gaudry, I865.
Species.-The genotype is the only species hitherto described.
Skull.-The frontals are quite flat, even along the suture. The fronto-parietal suture is on the same level as the hinder margin of the horn-cores. The parietal has a rounded upper surface with no trace of ridges for the temporalis muscle. In cross-section the horn-cores are oval, the narrower end being the anterior. They are widely separated at the base, and appear to be straight, continuing in the plane of the face. The foramina above the orbits are small. They are not sunken in depressions. There is a broad, but shallow, lachrymal fossa.

Dentition.-The upper molars all have short, fairly stout basal pillars. In comparison with the molar series the premolar series is relatively long. The inner wall of $P^{2-3}$ is indented, but there are no spurs projecting into the central cavity.

The lower teeth appear to vary somewhat. The diastema between $I^{3}$ and $P^{2}$ is exceptionally long. It has a considerable range of variation, however, to judge by the two specimens $\mathrm{M}_{12984}$ and M 13069 . In the former the length of the diastema, measured from the dental foramen to $P^{2}$, is 44 mm ., whereas in the latter specimen, which has the premolar series of the same length as the former, this distance is 31 mm . The external wall in $P^{3-4}$ shows a somewhat marked indentation in the posterior part of the tooth.

Comparison and Remarks.-The small and widely spaced horns distinguish the genus Graccoryx from all other Pontian antelopes. The absence of a definite keel, and of the frontal swelling which frequently unites the juxtaposed anterior keels in Tragocerus, sufficiently distinguishes it from that genus. The horn-cores are more like those of Psendotragus or Pachytragus, but they are smaller, straighter, and much less upright. In the case of Protoryx these differences are still more pronounced. In the retarded hypsodonty ; the strongly ribbed molars; the length of the premolar
series ; and the backward tilting of the horns; Graecoryx is more like Palacoryx: but the spacing of the horns; the large size of $P^{2}$; and the length of the muzzle ; distinguish it from that genus. By the length of the muzzle it differs from every antelopine genus we have seen except Damaliscus. In the latter genus the folding of the enamel in the upper molars affords one sufficient distinction, to say nothing of the others which exist. In the profile of the skull and the backward tilt of the horncores, Graecoryx resembles Tragoreas oryxoides; but the horns are much smaller, and the frontals are broader in proportion. The absolute length of the cheek-teeth series much exceeds that of T. oryxoides; and the length of the premolar series is, in proportion, even greater than it is in that species.

In thus removing the species Tragocerus valenciennesi from the genus in which it was placed by Gaudry, we are conscious that the material now at our disposal, though more perfect than that studied by Gaudry, is not enough to permit of a complete diagnosis, or even to determine the exact affinities of Graecoryx.

When Gaudry wrote his classic memoir but few Pontian antelopes had been discovered, and the objections to uniting Tragocerus amalthea with this form were not obvious. The better of the two specimens figured by him (op. cit., pl. xlviii, fig. 2) consists of little more than the frontlet with the horn-cores. It has no teeth. Now, however, the case is different: the genus Tragocerus has been recognized over a large part of Southern and Central Europe, in Asia Minor, and in China. Its numerous species are distinguished from those of all other genera of antelopes by their narrow horn-cores. These have an elongate sagittal diameter, their sharp anterior keels almost meet on the forehead, and are frequently connected by a marked transverse frontal swelling. A species without these universal characteristics cannot find a place in the genus, and misconceptions can only arise if it be allowed to remain there.

Without insisting upon the exact affinities of the genus Graecoryx, we incline to the idea of a probable relation to the Pseudotraginae, and this despite the backwardly directed horns and brachyodont teeth.

Derivation.-The name Graecoryx is derived from Грackós belonging to the Greeks, Grecian, and öpu乡 antelope, gazelle.

## Graecoryx valenciennesi Gaudry.

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\text { (PI. VIII, figs. 2, } 3 \text {; IX, I, 4, 5.) }
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r865. Tragocerus valenciennesi Gaudry, " Anim. Foss. Attique," p. 288, pl. xlviii, figs. 2, 3.
Diagnosis.-The characters of this, the only known species, are those of the genus.

Lectotype.-The frontlet described and figured by Gaudry (op. cit., p. 288, pl. xlviii, fig. 2) is hereby chosen as the holotype of the species. It is preserved in the Natural History Museum at Paris.

Localities.-The type-locality is Pikermi. The species is also known from Samos.

The species has been recorded from Croix-Rousse, Lyons (Depéret, 1887, p. 247, Tragocerus aff. valenciennesi).

Remarks.-Until now this species has been known only by the two specimens from Pikermi described and figured by Gaudry (1862), and by the fragment from Croix-Rousse described and figured by Depéret (1887).

In the Woodward collection from Pikermi there is a skull, M II430, which shows the frontals, the broken horn-cores, the right orbit, and the palate with the complete cheek dentition on either side. The specimen lacks the hinder portion of the braincase ; the face, as well as one horn, is badly crushed. We have, however, no hesitation in identifying it with Gaudry's species. A second specimen, also crushed, shows the right horn-core and the base of the left, but lacks the face, teeth, and braincase. A third specimen is a broken frontlet of a young individual with the right horn-core preserved.

In the Major collection from Samos is a frontlet, M, 4195, which, though the horn-cores are somewhat crushed and broken, seems referable to this species. Major (1894, p. 4) recorded the species from Samos, probably on the evidence of this specimen, since the name does not occur in the Catalogue of Samos fossils in the Museum at Lausanne.

The Woodward collection also contains numerous isolated specimens of both the upper and lower dentition.

As will be seen from the measurements on page 57 , the skull, M II430, is slightly larger than the holotype, but, since the several specimens of teeth vary in size, this difference need not be considered of importance. The genus Graecoryx agrees with Tragocerus in the small degree to which the face is bent down on the basicranial axis. The amount of bending appears to be somewhat greater than in Tragocerus amalthea, since the angle between face and brain-case is as much as $30^{\circ}$. It is possible that this figure may be exaggerated by crushing.

The oval cross-section of the horn-cores in Graecoryx is in marked contrast to that of the horn-cores of Tragocerus. In the latter genus there is a prominent anterior keel. The horn-cores themselves are tilted back more than they are in Tragocerus amalthea; their divergence appears to be trifling, and in any case it is much less than in Tragocerus.

The orbit, though crushed in the skull M II430, is seen to be approximately circular in another specimen (M II487). Its anterior margin lies over the midline of $\mathrm{M}^{3}$. This is its position in T. amalthea.

It is a remarkable fact that all the skulls or frontlets of this species preserved in the British Museum have one or both of the horn-cores much crushed laterally ; one is tempted to wonder whether this is due to some inherent weakness or lack of solidity.

The permanent upper dentition of skull M II430 is shown on pl. IX. The teeth are more brachyodont than in Tragocerus amalthea, in fact they seem to be almost, if not quite, as brachyodont as in Palaeoryx. The external ribs are decidedly stronger than in T. amalthea. Relative to the molar series, the premolar series is much longer than it is in the latter species.

A mandible (M I3069) with the permanent dentition is figured on pl. VIII. It resembles that of $T$. amalthea except for the relatively greater length of the premolar series; this is absolutely equal to, or longer than the length in that species, although the molar series is considerably shorter. The teeth are narrower and shorter in the crown than they are in Tragocerus and the ribs are more pronounced. The two posterior wings of $P_{3}$ and $P_{4}$ become united after an even smaller amount of wear than in $T$. amalthea.

Specimens showing the milk dentition of the upper jaw, M II450, and of the lower jaw, M 12989 , are figured on pl. IX.

## List of Specimens.

Note.-Except for the first item, these are all Woodward Colln., Pikermi.
M 4195. Frontlet with right horn-core crushed, and left horn-core somewhat broken near the base. Samos. Major Colln.
M II430. Imperfect skull with frontlet and teeth well shown, but lacking occipital region. Dentition figd. pl. IX, figs. 5, 5a.


M 12992. Frontlet, lacking left horn-core.
M ir43I. Palate lacking $P^{2}$.
M II450. Left maxilla of an immature individual with $d m^{3-4}$ in place and $M^{1-3}$ in an early stage of wear; $P^{2}$ has just been cut and is quite unworn. Figd. pl. IX, figs. 4, $4 a$.
M II45I. Left maxilla of a very young individual with $d m^{2-4}$ in place and $M^{2}$ quite unworn.
M II452. Left maxilla with complete cheek dentition.
M II458. Left maxilla lacking $P^{2}$.
MII487. Right side of face showing orbit, portion of lachrymal fossa, and $M^{2-3}$.
M 12986 . Left maxilla with complete cheek dentition.
M 12988. Right maxilla of an immature individual with $d m^{3-4}$ in place and $M^{1-2}$ in an early stage of wear, other teeth wanting.
M 12995. Left maxilla of an immature individual with $d m^{3-4}$ in place and $M^{3}$ quite unworn.
M II457. Left mandibular ramus of an immature individual with two incisors, the crowns of $d m_{2-4}$ broken, $M_{1-2}$ in an early stage of wear, and $M_{3}$ only partly cut.

M ir 460 . Right and left mandibular rami with complete cheek dentition in an early stage of wear.


M ir 499. Right mandibular ramus of an immature individual, $P_{3}$ almost unworn, $d m_{ \pm}$much worn, $M_{1-3}$ in an early stage of wear.
M irjor. Left mandibular of a young individual with $d m_{3-4}$ in place and $M_{2}$ only partly cut.
M iI506. Fragmentary right and left mandibular rami of a young individual with $d m_{2-4}$ and $M_{1 \cdot 2}$.
M I2983. Three fragmentary mandibular rami.
M r2984. Part of left mandibular ramus, from the symphysis backwards to $P_{4}$. Diastema between $I_{3}$ and $P_{2}$ approximately 79 mm . Pl. VIII, fig. 2.
M r2989. Right mandibular ramus, similar to M I3070. Pl. IX, figs. I, га.
M I2990. Left mandibular ramus with $P_{4}$ to $M_{2}$.
M 12993. Right and left $P_{2}$.
M r 3069. Right mandibular ramus complete from the symphysis backwards to $M_{3}$, teeth in a medium stage of wear. Pl. VIII, figs. 3, $3 a$.
M 13070. Left mandibular ramus of a young individual with $d m_{2-4}$ in place and $M_{2}$ only partly cut.

## Subfamily BUBALIDINAE.

" Skull long and slender, with or without lachrymal fossa, without ethmoidal vacuity. Horns pushed far backward, usually roundish in cross-section and more or less spiral. Teeth usually hypsodont, without basal pillar." (Schlosser, 1925.)

## Genus CRIOTHERIUM Major.

I890. Lydekker, R., Nature, XLIII, p. 86, genus caelebs. (ex Major MS.).
1891. Major, C. I. Forsyth, C. R. Acad. Sci. Paris, CXIII, pp. 608-6og.

Diagnosis.-Bubalidinae of large size, with long, high, narrow muzzle ; face bent down at right angles to the basicranial axis ; parietals in the same plane as the occipitals ; tympanic bulla of medium size, tapering posteriorly ; no ethmoidal vacuity, lachrymal fossa very small. Horns situated considerably behind the orbits, short, the right horn forming a close clockwise spiral of about one revolution, cross-section almost circular at the base, becoming narrowly elliptical further up, with a strong posterior keel, anterior keel weak or absent. Dentition hypsodont; premolar series short ; molars without basal pillars, and with rather weak external ribs ; enamel rather rugose.

Genotype.-Criotherium argalioides Major, i89I.
Remarks.-Schlosser, who has given the only detailed description hitherto, considers that this curious form should be included in the Bubalidinae. The undoubted resemblance to Connochaetes in certain respects and to Damaliscus in others renders this classification quite plausible, though it would be unwise at present to insist on the genetic affinity.

The alliance between Criotherium and Urmiatherium which Schlosser (1904, p. 27) suggested, has now been disposed of by de Mecquenem's discovery at Maragha of a fine skull of the latter (de Mecquenem, 1925, p. 42). From this it appears that Urmiatherium is related to Ovibos.

## Criotherium argalioides Major.

1891. Criotherium argalioides Major, C. R. Acad. Sci. Paris, CXIII, p. 60 .
1892. Criotherium argalioides Major, Schlosser, Beitr. Paläont. Geol. Oest.-Ung., XVII, pp. 23-28.

Diagnosis.-This is the only speries. The characters are those of the genus.
Lectotype.--In his original description Major (1891, p. 609) does not give any particulars concerning the material on which this species is based. His next work ( 1892 , p. 95) speaks of " plusieurs crânes magnifiques" : again he does not specify a type. His paper of 1894 is largely a reprint of the preceding. At the end is a list of specimens which is headed "Catalogue d'Ossements Fossiles recueillis à Mitylini (Ile de Samos) et déposés au Collège Galliard, à Lausanne." That this list is of no value, and was never intended for publication, appears from a letter addressed to Major by Prof. Renivier. The letter, dated 28 April, I893, is preserved in the library of the Geological Department of this Museum, and from it the following extract is taken.
" Je passai à l'imprimerie pour . . . donner mes indications, et feuilletai le catalogue.
"Quelle fut mon étonnement en voyant que cette liste était par ordre de Nos., ne correspondant à l'ordre zoologique que dans les premières pages, mais ensuite une vraie salade donnant pèle-mèle les echantillons d'Hipparion, de Samotherium, des Gazelles, etc., comme on les avait inscrit au fur et à mesure de leur nettoyage. J'y vis également des Nos. portant cette seule mention 'donné au Musée de Genève,' ' au Musée de Lausanne,' etc."

This extract proves that the list in question is only a rough working copy, and as such it may be disregarded.

The finest series of skulls is that about to be described. It was acquired from Dr. Major during the years $1889-\mathrm{I} 890$, that is before any description was published. There is no doubt that the specimens formed part of Major's original series and that it is permissible to choose one of them as the holotype.

The skull with the registered number M 4199 is hereby chosen as the holotype of the species Criotherium argalioides, and the skull registered M 420I as the paratype.

Locality.-The type locality is Samos. None other is known.
Skull.-Major described the general aspect of the skull and horns very briefly
when (1891, p. 609) he first mentioned this form. To this description nothing was added until 1904 when Schlosser described a skull preserved at Munich. Schlosser's account (1904, pp. 23-28) is as full as his material allowed. Owing to closure of the sutures, and to abrasion of the outer tables of the bones there were certain areas, the structure of which remained obscure. Fortunately there are three skulls (M 4199, 4200, 420I) in the British Museum collections which have made it possible to ascertain the shape and relationships of every bone


Fig. I. -- Criotherium argalioides Major. Skull seen from below. Paratype. M4200, B.M. (Geol. Dept.). $\quad \frac{1}{4}$ nat. size. Mitylini, Isle of Samos. with few exceptions. The accompanying figures illustrate the structure of the face, brain-case, basi-cranium and palate.

The basi-cranium is best shown in M 4200. The basi-occipital is oblong, the ventral surface consisting of two semi-cylindrical ridges which extend in an antero-posterior direction. Posteriorly these ridges bear a facet for articulation with the atlas, an arrangement which is always present to a greater or less extent among those animals capable of a large range of dorso-ventral movement of the head. A prominent transverse ridge just in front of the facet is for the articular capsule. Anteriorly each longitudinal ridge bears a well-marked scar for the rectus capitis muscle. The paroccipital processes are massive pyramidal structures. In every specimen they are broken off short so that it is not certain what the prolongation was like. Immediately in front are the moderately inflated wedge-shaped bullae. The anterior processes are broken away, but there seems to be evidence that they passed inward along the anterior wing of the basi-occipital, and then forwards along the descending wing of the alisphenoid. Owing to damage it is not possible to delimit the tympanic, petrosal, and mastoid. Taken together they form a high compact mass, roughly of triangular shape, which is fixed in between the paroccipital and post-glenoid processes, and which completely overtops the latter. The general appearance of this region is shown in the accompanying text-figure.

The inferior surface of the squamosal bears an oblong glenoid fossa and a relatively weak post-glenoid process. Both are of the usual ruminant type. The relationships of pterygoid, alisphenoid, and palatine are not certain. The palatal laminae of the palatines extend forward to the front of the third molar, or very slightly beyond. The palatal portions of the maxillae are incomplete anteriorly ; the part preserved does not show any features worthy of comment. Only the extreme posterior tips of the median processes of the premaxillae are preserved. They are pointed.

The bones of the brain-case and face are best shown in M 4199. Only the occiput-the occipital and the posterior portions of the parietals-is better shown in M 4201 .

Seen from behind, the occipital is roughly semi-circular in shape. It lies in a plane almost at right angles to the plane of the palate. The scars for the ligamentum nuchae and for the various muscles of the neck are well marked (especially in M 4r99, and M4200). The parietals have been pushed back out of the roof of the braincase and lie entirely at the back and sides; the hinder portion is in the same plane as the occipital. They have the form of a narrow scalene triangle of which the longer limb runs round the side of the cranium inside the temporal fossa. The


Fig. 2.-Criotherium argalioides Major. Skull seen from left side. Lectotype. M 4 I99, B.M. (Geol. Dept.). $\frac{1}{\frac{1}{2}}$ nat. size. Mitylini, Isle of Samos.
alisphenoids are of no special interest; their boundaries are very indistinct and uncertain. Similar conditions obtain with regard to the pterygoids and orbitosphenoids.

The nasals are unusually thick and heavy. They are bluntly pointed anteriorly and broaden gently as they pass backwards to the level of the anterior margins of the lachrymal and jugal, reaching their widest point above the contact between $M^{2}$ and $M^{3}$. From this point they taper off to their posterior extremity just above the anterior margin of the orbit.

The frontals are the largest bones in the skull. They extend from the widest part of the nasals to the flattened and perpendicular occiput. Their anterior angle is moderately blunt and truncated. On the nasal border they tend to be slightly inflated, a tendency which becomes more marked where the frontal joins its fellow
of the other side. At the back of the skull each bone is bent at a right angle, and passes downwards to meet the parietal, and so form part of the posterior wall of the brain-case. It is on, and immediately in front of, this change of direction that the horn-cores are situated. Between the horns the suture forms a high swollen ridge. The surface of the frontals is gently concave, the depression passing outwards and downwards from the middle line of the skull to merge into the lachrymal fossa.


Fig. 3.-Criotherium argalioides Major. Skull seen from the front. Lectotype. M 4 I99, B.M. (Geol. Dept.). $\frac{1}{4}$ nat. size. Mitylini, Isle of Samos. The supra-orbital foramen is small. Approximately two-fifths of the orbit is enclosed by the orbital margin of the frontal. This margin is not produced in the manner frequently found in other ruminants. The frontal portion of the post-orbital bar-the post-orbital process of the frontal-is small and slender.

The horn-cores are very short, sub-circular in cross-section at the base, becoming narrowly elliptical at the summit. The strong posterior keel, which greatly facilitates the tracing of the clockwise twist of about one revolution, is very broad, thin, and sharp. There appears to be evidence that the keel continued round on to the outer side of the base of the horn-core, and finally died out on the surface of the frontal just above the post-orbital bar. In addition to the main keel there are one or more subsidiary ones. These are very well seen in M 4199. In this skull there are three knifeedged keels which start on the postero-medial surface of the horn and follow sub-parallel courses with an interval of about 8 mm . between each keel. Approximately one-third of the distance to the tip the centre keel dies out, or else is broken away, it is not clear which alternative is correct, but the other two gradually run together and merge with the main keel at the tip of the horn. Two or, possibly, three other keels have their origin on the antero-internal surface of the horn. They pass obliquely upwards and outwards across the front and then, when they reach the outer surface, follow an almost perpendicular course to the summit. That these features are very variable is well shown by this one specimen, M 4199. On the left horn-core only two out of the three keels in the first group are present. They appear to correspond to the two lower ones of those on .the right horn-core. The lower one, allowing for accidents of preservation, agrees with its fellow of the opposite side, whereas the upper one extends further towards the summit. Of the second group, that arising from the antero-internal surface,
it is not possible to say anything ; it has been much damaged. The other specimen with the horn-cores preserved, M 420I, shows two faint keels arising from the postero-medial surface, but there is no trace of any on the antero-internal surface.

The facial portion of the lachrymal is an oblong, concave plate of bone. It has a blunt, rounded, anterior margin ; posteriorly it forms the superior anterior margin of the orbit, about one-fifth of the whole circumference. Inside the orbit, the lachrymal is composed of two very distinct regions. The first of these is rectangular, and pierced by the lachrymal foramen; it forms the antero-superior wall of the orbit. The other region is an inflated, bullate, thin-walled expansion which is closely applied to the jugal and projects far back in the orbit towards a process composed of parietal, squamosal, alisphenoid, and orbitosphenoid : in this manner the orbit is provided with a large extent of bony wall.

The jugal is, relatively, a small bone. The facial portion, which is of approximately the same extent as that of the lachrymal, is concave above, where it takes part in the formation of the lachrymal fossa, and convex below. The zygomatic process is straight and fairly stout. At its posterior end there is a small ascending branch which forms the lower part of the post-orbital bar. A ridge which originates in the upper region of the facial portion passes downwards and backwards to merge into the inferior margin of the orbit. The jugal or inferior margin of the orbit is about two-fifths of the whole.

The maxilla rises almost perpendicularly from the alveolar border as far as a plane which passes, approximately, from the highest point on the orbital border of the jugal to the top of the infra-orbital foramen. Above this it rises rapidly upwards and inwards to the nasals. The hinder margin sends a short process into a notch in the jugal, another process fills the re-entrant angle between the lachrymal and the jugal. A slight concavity in the region of the latter process forms part of the lachrymal fossa. The infra-orbital foramen is far forward, and low down on the maxilla: it is just above the roots of $P^{2}$.

Three things distinguish the skull when regarded as a whole. These are the long, straight, high, and narrow muzzle; the almost disproportionately small zygomatic arches and post-orbital bars, both of which are unusually close to the long axis of the skull ; and, lastly, the short and strongly twisted horn-cores placed right at the back of the head, immediately above the vertical occiput.

Dentition.-There is little or nothing to add to the account of the teeth given by Schlosser (1904, pp. 24-26). The premolars are less hypsodont than the molars. There is no basal pillar to the upper molars but its position is occasionally occupied by a small tubercle. This tubercle may occur on any tooth on either side of the mouth. It need not be present, and if it is, it is not necessarily found in the corresponding tooth of the other side. In skull M 4199 such tubercles are developed on left $M^{3}$ and right $M^{2} ; \mathrm{M} 4200$ has the same feature faintly shown on $M^{1}$ of both sides.

Remarks.-Schlosser has mentioned two distinct types of premolars in this species: a large and a small. Both can be recognized in the four skulls in the British Museum. It is difficult to imagine that they do not represent at least two
races. It is not possible to say what other differences, if any, were correlated, and we do not propose to distinguish these two types by separate names.

In the Major collection at Lausanne is a fine skull of this species (cat. no. 79) with the mandible attached. There is, therefore, no uncertainty as to the association of the upper and lower dentition. The characters of this mandible agree with those of the mandibles which Schlosser has assigned to this species and figures, and the British Museum mandibles are similar. The Lausanne specimen belongs to the variety with long premolars. The dimensions are,

$$
\begin{aligned}
& \text { Length of molar series .. .. .. .. .. .. .. .. . . } 85 \text { mm. } \\
& \text { premolar series .. .. .. .. .. .. .. .. } 46
\end{aligned}
$$

Unfortunately the frontal region with the horn-cores, as well as the occipital region, is in too poor a state of preservation to permit one to form any opinion as to the possible correlation of differences of cranial structure with the shortness of the premolar series.

Similar conditions obtain among the British Museum specimens. M 4199 has good sutures and poor teeth; in M 4200 the sutures are closed and the teeth are poor; in M 4201 the teeth are very good but the sutures are poor: a fourth skull, M 4202, not previously mentioned, agrees with $M 4201$ in that the teeth are good and the sutures poor. There is, however, one fact which comes out of a study of the British Museum series, namely this. The two skulls M 4200 and M 4202 both belong to the form with a short premolar series; they both differ from the two with long premolar series, M 4199 and M 420I, in the forehead which is gently convex from side to side, and on which the concavities found on either side of the median ridge in M 4199 and 4201 are indicated by areas which are flattened or only very slightly concave. The median ridge in these two skulls is not developed.

Since all four skulls are more or less crushed it is not wise to place too much reliance on these features, but it is worth while to point out that, generally speaking, M 4200 and M 4202 have every appearance of being coarser and of heavier build. This difference may be sexual, or it may be further evidence in support of the view that there are two races.

De Mecquenem ( I 925 , pl. v, fig. 8) has figured from Maragha the mandibular ramus of a large antelope, but has not assigned it to any definite genus. The premolar series in this ramus is even shorter than in the Lausanne specimen, but the character of the dentition is remarkably similar, and it is extremely probable that the Maragha ramus belongs to Criotherium argalioides.

## List of Specimens.

All from the Major colln. from Samos.

## i. Skulls with long premolar series.

M 4199. A skull, well preserved except for the face being somewhat crushed laterally; cheek dentition much worn and premolar crowns broken on the left side. The lectotype of the species.

M 420I. A skull, well preserved except for the face being somewhat crushed laterally; complete cheek dentition in an early stage of wear. The right maxilla with a supernumerary $P^{2}$ impacted between $P^{2}$ and $P^{3}$. The skull is slightly larger than that figured by Schlosser. The paratype of the species.
Length of the cheek teeth series .. .. .. .. .. .. .. $\mathrm{mm}_{5}$
Length of the premolar series .. .. .. .. .. .. .. .. 47
ii. Skulls with short premolar series.

M 4200. A skull with the horn-cores broken off close to the frontal, but otherwise in a fine state of preservation, showing well the occiput, basicranium, zygoma and face; dentition in an advanced state of wear, and lacking $P^{2}$. This is almost exactly the same size as the Munich specimen.

| Length of the cheek teeth series | .. | . | .. | . | .. |  | mm. |  |  |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | ---: |
| Length of premolar series | .. | . | .. | .. | .. | .. | .. | .. | 4 r |

M 4202. A skull lacking the occiput and part of the right horn-core ; basicranium and lateral regions of the brain-case badly broken; teeth moderately worn.

M 4206. Palate with the complete cheek dentition on the right side. It agrees almost exactly in size with M 4200, and with the Munich specimen.

iii. Fragments of upper and lower jaws.

M 4306. Left maxilla with two molars and apparently associated $P^{2}$ and $P^{3}$.
M 4207. Three mandibular rami with $P^{4}-M^{3}$ in a medium stage of wear. These belong to the series with short premolars. $P^{4}$, as Schlosser has observed, is simple in structure.
M 4208. Right mandibular ramus of a young individual with $d m_{4}$ in place, $M_{1}$ in an early stage of wear and $M_{2}$ just being cut.

## Genus PRODAMALISCUS Schlosser.

1904. Beitr. Paläont. Geol. Oest.-Ung., XVII, p. 29.

Diagnosis.-Bubalidinae of large size with elongate skull, the face bent down on the basicranial axis at an angle of $135^{\circ}$. Horn-cores widely separated, 45 mm ., strongly divergent, oval in cross-section. Premolars simple; molars without basal pillars.

Genotype.-Prodamaliscus gracilidens Schlosser (1904, pls. iv, v, vi).

## Prodamaliscus gracilidens Schlosser.

1904. Prodamaliscus gracilidens Schlosser, Beitr. Paläont. Geol. Oest.-Ung., XVII, pp. 29-31, pls. iv (i), 4 ; v, (ii), $5,7,8$, II, I2 ; vi (iii), 4 .
Diagnosis.-This is the only species ; the characters are those of the genus.
Holotype.--The skull described and figured by Schlosser (op. cit., pl. iv (i), 6 ; vi (iii), 4). It is preserved in the Munich museum.

Locality.-The type locality is Samos. None other is known.
Remarks.-Schlosser places this species very near to Alcelaphus palaeindicus (Falconer) and near to the line of descent of the recent African genus Damaliscus. He is careful to point out that it is not truly ancestral, but that it is very close indeed to what the ancestral form of Damaliscus must have been like.

## Subfamily HIPPOTRAGINAE.

Diagnosis.-" Skull long, cranial axis bent. Ethmoidal vacuity present; lachrymal fossa absent. Horns over the orbits curved or straight, always of considerable length, and roundish in cross-section. Teeth hypsodont, with strong basal pillars ; in the older forms brachyodont, with only weak basal pillars." (Schlosser, 1925.)

## Genus MICROTRAGUS Andree.

1865. Palaeoryx Gaudry pars, Anim. Foss. Attique, p. 276.
1866. Microtragus Andree, Palaeontographica, LXVII, p. I50.

Diagnosis.-Hippotraginae of medium size with short face and moderately long brain-case ; face bent down at right angles to the basicranial axis ; summit of frontals extremely high ; facial profile forming an angle near the fronto-nasal suture ; frontal suture swollen ; orbits far forward ; shallow lachrymal fossa ; no ethmoidal vacuity ; supra-orbital foramina not sunken ; skull broad at the orbits, narrow in the occipital region ; tympanic bulla rather small, elongate and tapering; horns large, rather upright, moderately or strongly curved, with an elliptical cross-section, elongate antero-posteriorly; dentition moderately hypsodont, ribs of moderate strength, basal pillars either absent or inconstantly developed, premolar series moderately short.

Genotype.-Microtragus schafferi Andree, 1926.
Species.-The species and varieties recognized here are M. parvidens (Gaudry), M. parvidens var. schafferi Andree-the genotype, M. parvidens var. gaudryi nov., and M. ? stützeli (Schlosser).

Remarks.-This genus was founded by Andree (1926, p. I50) on a skull from Samos which he described and figured under the name of Microtragus schafferi. Before Andree's memoir appeared Dr. Pilgrim had already decided that it was expedient to place the species Palacoryx parvidens, the type of which is the skull from Pikermi described and figured by Gaudry (1865), in a separate genus of its own. Andree's
species Microtragus schafferi, is, however, so closely allied to Palaeoryx parvidens that it seems quite impracticable to separate them generically. For this reason we refer the Pikermi species to the genus Microtragus Andree. Gaudry himself suggested (1865, p. 277) that when the species was better known it would possibly have to be separated as a distinct genus. Schlosser (I904, pp. 36, 86) implied a certain amount of dissatisfaction with the generic position, but did not change it. The time seems to have arrived when Gaudry's suggestion may take effect.

There are not less than seven skulls from Pikermi which are referable to this genus: two in Paris, four in London, and one in Munich. The holotype of Microtragus schafferi from Samos is in Vienna, and has, unfortunately, not been seen by us. The skull preserved at Münster, described and figured by Andree (1926, p. I62, pl. xi, fig. II, pl. xv, fig. 2), cannot, we think, belong to the species $M$. parvidens ; the altogether different facial profile and the shorter brain-case indicate that it cannot even be placed in the same genus. Possibly it is a species of Palaeoryx smaller than P. pallasi.

The variations of these seven skulls of Microtragus amongst themselves have caused us to wonder whether it is feasible to recognize any specific distinctions between them. We have, however, decided, while keeping them all in the one species $M$. parvidens, to refer three of the skulls in the British Museum (M 10833, MII428, and M 13067) to M. schafferi as a distinct variety, mainly on account of the shorter occiput and the smaller degree to which the face is bent down on the basicranial axis. We refer the skull in the British Museum registered M II4I7 to M. parvidens. For a second skull preserved in Paris we propose a second varietal name. This specimen has a longer brain-case and less divergent horns than the type. It is possible that the Munich skull of $M$. parvidens may belong to this variety. The dimensions of all these specimens have been collected in a table on p. 79. We have paid no attention to any variation in the width of the skull at the orbits, because we regard this character as sexual.

It seems probable that Palaeoryx stützeli Schlosser may also belong to Microtragus. It is represented by a very imperfect skull in Munich which does not permit the crucial points to be ascertained, but, as pointed out by Schlosser ( 1904, p. 43), it resembles $M$. parvidens in the situation of the horns and in the swelling of the frontal suture. This specimen is rather smaller than those referred to M. parvidens, especially in the horn-cores which have also a more circular cross-section. Andree, however, has referred to Palaeoryx stützeli a skull in which the horn-cores are more elongate than they are in the holotype. The dentition referred by Schlosser to $P$. stützeli is more brachyodont, and the upper premolars are longer, than in the species of Microtragus, moreover the internal wall of both $P^{2}$ and $P^{3}$ is indented.

Although Microtragus parvidens is closer to Palaeoryx woodwardi than it is to $P$. pallasi, yet it differs from both by its upright, curved horns and long brain-case. Microtragus agrees with Protoryx in the shape and position of the horns and the height of the tooth-crowns, but differs from it in the swollen frontal suture and the forward position of the orbits. The profile of the face and the elevation of the frontal summit above the basicranial axis distinguishes it, not only from Palaeoryx
and Protoryx, but also from all other antelopine genera except Hippotragus. In that genus, however, the external ribs of the upper molars are very prominent and there are large basal pillars ; moreover, the frontal suture is not swollen, there is no lachrymal fossa and the frontal diameter is relatively less.

Although, in the present state of our knowledge, it is not advisable in most cases to express very decided views as to the group in which any particular genus of antelope should be placed, yet we are inclined to disagree with Andree in his opinion that Microtragus should be classified with Pseudotragus. The resemblances to the recent genus Hippotragus, on which Andree has failed to comment, seem to be very significant, and to suggest that Microtragus belongs to the Hippotragine group rather than to the Pseudotragine group.

## Microtragus parvidens Gaudry.

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\text { (Pl. VII, figs. } 3,3 a .)
$$

186ı. Palaeoryx parvidens Gaudry, C. R. Acad. Sci. Paris, LII, p. 241.
1861. Palaeoryx parvidens Gaudry, Bull. Soc. Géol. France, [2], XVIII, p. 388.
1865. Palaeoryx parvidens Gaudry, Anim. Foss. Attique, p. 276, pl. xlvii, figs. 6, 7.

Non Palaeoryx parvidens Andree, 1926, Palaeontographica, LXVII, p. 162, pl. xi, fig. II; pl. xv, fig. 2.
Diagnosis.-A Microtragus with the face bent down at an acute angle on the basicranial axis. Horn-cores elliptical in cross-section, elongate antero-posteriorly. Lachrymal fossa distinct but shallow.

Lectotype.-.The skull from Pikermi described and figured by Gaudry (r865, pl. xlvii, figs. 6, 7) is chosen as the holotype. It is preserved in the Natural History Museum at Paris.

Locality.-The type locality is Pikermi. Up to the present it does not appear to be recorded from Samos.

Remarks.-A skull from Pikermi in the Woodward Collection from Pikermi (M II4I7, pl. vii, figs. 3, $3 a$ ) lacks the occipital bones and the upper half of the horncores: it has the entire cheek dentition preserved, though in an advanced state of wear. This skull agrees fairly closely with the type of this species (Gaudry, I86I, 1865), except that the cranium is more stoutly built, the width at the orbits being markedly in excess of that dimension in the Paris skull, and that the cross-section of the horn-cores is more broadly elliptical. These differences we are inclined to ascribe to sexual or individual variation. It may be mentioned that the right and left horn-cores of the holotype do not correspond in their dimensions, their sagittal and transverse diameters being respectively 49 mm . and 35 mm . for the right horncore and 45 mm . and 38 mm . for the left horn-core. We are unable to say which of these should be regarded as the standard shape. The measurements of the British Museum skull are given on page 79, side by side with those of the holotype and of other skulls referable to Microtragus, as well as with those of certain species of Palaeoryx for comparison.

The face is bent down on the basicranial axis at an acute angle as in the holo-
type. This angle is obtuse in the variety schafferi (see its holotype and British Museum M 10833).

The horn-cores are elliptical in cross-section and elongate antero-posteriorly, thus resembling Protoryx rather than Palaeoryx pallasii; the axis of maximum elongation is oblique to the antero-posterior axis of the skull. They are much more upright than are those of Palaeoryx and arise at a right angle, or even obtusely to the parietal surface. In this respect they differ markedly from Palaeoryx in which this angle is acute. Unlike the horn-cores of Palaeoryx they have a pronounced backward curvature, much as in Protoryx, the horn tips being very nearly over the occipital crest when the basicranial axis is horizontal ; the curvature is, however, much less than in Microtragus schafferi Andree. The degree of divergence of the horn-cores is about the same as that in Protoryx carolinae. All the British Museum skulls show a similar divergence, as does also the holotype of var. schafferi, but in the second skull in Paris, described below as a distinct variety, the horn-cores are much more nearly parallel. As Gaudry has remarked, the horn-cores are both stouter and longer in proportion to the size of the teeth, and to the parietal and occipital widths than they are in Palaeoryx pallasii, but, as might be expected, the skull is wide in the frontal region.

The face is rather short ; its profile falls very steeply towards the front from the summit of the frontal to a point a little in advance of the fronto-nasal suture, after which the descent becomes more gentle. This feature is correlated with a quite exceptional height of the frontal summit above the plane of the teeth, also with an exceptionally forward position of the orbit, the anterior margin of which lies over the middle of $M^{3}$ instead of just behind it as in Palaeoryx. The height of the frontal is decidedly less in M Io833, which seems to agree in this respect with the variety schafferi. The frontal suture is strongly swollen everywhere, a feature remarked by Schlosser in Palaeoryx (Microtragus?) stützeli, and which is not found in undoubted species of Palaeoryx. There is a very distinct lachrymal fossa, though Schlosser (1904, p. 36) has stated that it is absent ; it is, however, rather shallower than in P. pallasii. The supra-orbital foramina are small and not sunken ; shallow grooves go forward from them to the lachrymal fossa. The nasals indent the frontal at an acute angle: in Protoryx and Palaeoryx the suture is M-shaped. The posterior ends of the nasals are opposite the anterior margin of the orbits. The orbits are approximately circular.

The brain-case narrows rather rapidly behind the horn-cores, and is out of proportion to the broad frontals and the strong horns ; it is relatively longer than in Palaeoryx. The occipital surface forms an obtuse angle with the parietal. The basioccipital agrees generally with that of Palaeoryx and Protoryx so far as can be seen. The tympanic bullae are not large but elongate, tapering behind.

The upper teeth are more hypsodont than those of Palaeoryx, and probably as high in proportion as those of Protoryx. On account of the advanced state of wear of the dentition in the skulls preserved in Paris and in London the height of the crowns of the teeth cannot be estimated with accuracy. It is assumed that they are as high as in the skull of var. schafferi (M 1o833). The external ribs are decidedly
less strong than they are in Palaeoryx. The specimens in the British Museum show no trace of a basal pillar in either the upper or the lower molars; Gaudry mentions one as present in $M^{1}$ of the holotype. The relative length of the premolars is not strikingly different from what obtains in Palaeoryx, but the internal wall of $P^{2}$ is not indented as it is in all known species of Palaeoryx.

## List of Specimens.

Note.-All are from Pikermi, Woodward Colln.
M II4I7. Skull lacking the premaxillary and occipital regions and the upper half of the horn-cores; the complete cheek dentition is present in an advanced state of wear. (Pl. VII, figs. 3, 3a.)
The following specimens are provisionally referred to this species.
M I3009. Right mandibular ramus with $P_{4}-M_{3}$.
M izoIr. Left mandibular ramus from the dental foramen to $M_{3}$ but with all the teeth, except $M_{2}-M_{3}$, broken off at the roots.
M I3OI2. Right mandibular ramus with $M_{1-3}$.

Microtragus parvidens var. schafferi Andree. (Pl. VlI, figs. 2, 4, $4^{a}, 4^{b}$.)
1926. Microtragus schafferi Andree, Palaeontographica, LXVII, p. 150, pl. xiv, figs. 2, 5, 6, 6a.

Diagnosis.-A variety of $M$. parvidens in which the face is not bent down on the basicranial axis to the same extent, the horn-cores are more strongly curved backward, and the brain-case is shorter than in the type.

Lectotype.-As holotype of this variety is taken the Vienna skull from Samos described and figured by Andree (1926, pl. xiv, figs. 2, 5, 6). It is preserved in the State Museum of Natural History at Vienna (Catalogue Number V, I).

Locality.-The type locality is Samos. The variety is also known from Pikermi.
Remarks.-This form, which was described as a separate species by Andree (1926, p. I50), has the face less bent down on the basicranial axis than in the holotype of $M$. parvidens; the height of the frontal above the basicranial plane appears to be less; the horn-cores are more curved, their tips reaching back over the occipital condyles when the basicranial axis is horizontal ; the brain-case is also slightly shorter. In every other particular it seems to conform with the holotype of $M$. parvidens, from which it cannot be separated generically, and, probably, not specifically.

There is in the British Museum a skull (M 10833, Pl. VII, figs. 4, 4a, 4b) which agrees with the holotype of $M$. schafferi in every particular in which that form differs from the holotype of $M$. parvidens. The horn-cores are imperfectly preserved in M 10833, but although in the frontlet M 13067 (Pl. VII, fig. 2), they do not seem to extend so far back as in the holotype, it is probable that the difference is
not great, and may be regarded as due to individual variation. The width at the orbits is greater in M 10833 than in the holotype, whereas in the frontlets M II428 and MI3067 this difference is hardly appreciable. The wider frontal is probably a sexual attribute.

The upper dentition in the holotype of $M$. schafferi is in a fairly advanced state of wear, and it is impossible to be at all certain as to the degree of hypsodonty. Andree has described it as brachyodont, but, in the absence of further information, we do not feel justified in assuming that the dentition of the Samos form is any less hypsodont than that of the Pikermi skull (M Io833, Pl. VII, figs. 4, 4a, 4b). The structure of the teeth seems to be very similar in the two skulls, but in M ro833 the molars have not the basal pillars which appear to be present in the holotype. In the specimen preserved in the British Museum the external ribs of the molars are stronger, and the premolar series is slightly longer than in the holotype of M. parvidens.

## List of Specimens.

Note.-All are from Pikermi. Woodward Colln.
M 10833. Skull, lacking only the upper half of the horn-cores and the premaxillary region. The dentition is in a medium stage of wear ; $P^{2}$ is broken off, as well as most of the teeth on the right side of the palate. (PI. VII, figs. 4, 4 a, $4^{b}$.)
MII428. Skull lacking the face, the teeth, and the upper part of the horncores.
M 13067. Frontlet with the right horn-core almost perfect. (Pl. VII, fig. 2.)

## Microtragus parvidens var. gaudryi nov.

1865. Palaeoryx parvidens Gaudry pars, Anim. Foss. Attique, p. 276.

Diagnosis.-A variety of Microtragus parvidens with longer brain-case and less divergent horn-cores than the holotype of the species.

Holotype.-The second skull mentioned but neither described nor figured by Gaudry ( 1865 , p. 276). It is preserved in the Natural History Museum in Paris.

Locality.-The type locality is Pikermi. The variety may also occur at Samos.
Remarks.-The dimensions of the holotype are given in the table on page 79.
This was the second of the two skulls referred by Gaudry ( $1865, \mathrm{p} .276$ ) to the species Palaeoryx parvidens and was not figured. Although Gaudry was probably right in not separating it specifically from the type, yet the distinctly greater length of the brain-case and the much smaller degree of divergence of the horn-cores seem to entitle it to be regarded as at any rate a distinct variety. These characters distinguish it even more markedly from the variety schafferi. The size of the horncores, the shape of their cross-section, and the width of the skull at the orbits are the same as in the type of the species.

No specimen in the British Museum conforms to this variety. It seems
possible, however, that a skull of $M$. parvidens in Munich may belong here, since the horn-cores stand closer together than in the holotype of that species, or in the skulls referred to var. schafferi, while, on the other hand, in this respect they resemble the holotype of var. gaudryi. The brain-case is incompletely preserved in the Munich specimen. For this reason a full comparison is not possible.

## Genus MICROTRAGUS ?

The following species, referred by Schlosser (1904, p. 4I) and Andree (r926, p. 162) to the genus Palaeoryx, differs from the other members of that genus in the characters of the horn-cores and in the swelling of the frontal suture. Since, in these two respects, it approaches Microtragus parvidens we place it with all reserve in the same genus.

## Microtragus? stïtzeli Schlosser.

1904. Palaeoryx stiitzeli Schlosser, Beitr. Paläont. Geol. Oest.-Ung., XVII, p. 4I, pl. viii, figs. I, 2, 6 .

Diagnosis.-A Microtragus? in which the cross-section of the horn-cores is sub-circular at the base becoming broadly elliptical towards the summit; horncores close together at the base and not widely separated at the tips.

Lectotype.-The specimen figured by Schlosser (1904, pl. viii, figs. 6, 6a, 6b) is hereby chosen as the holotype of the species. It is preserved in the Palaeontological Museum at Munich.

Locality.-The type locality is Samos. None other is known.
M.? stützeli has also been recorded from the following localities in Europe: Rumania, Taraklia, Bendery (Khomenko, 1913, p. 126) ; Ukraine, Tchobroutchi, Kherson (Pavlov, 1914, p. I82).

Remarks.-This species is very imperfectly known. The holotype and the specimen figured by Andree (1926, pl. xiv, figs. I, 3) are both without teeth, and the teeth figured by Schlosser as belonging to this species are so referred on circumstantial evidence.

## Genus HIPPOTRAGUS Sundevall.

1846. K. Svensk. Vet.-Akad. Handl., 1844, p. 196.

Diagnosis.-Large but slender hippotragine antelopes; horns over orbits, strongly recurved, long, slightly but regularly divergent, rounded in cross-section. Teeth brachyodont to hypsodont, basal pillars weak to strong.

Genotype.-Antilope leucophaea Pallas (i766, Misc. Zool., p. 4).
Nomenclature.-The name Hippotragus is antedated by Ozanna Bechstein, 1845. Since the latter name is all but unknown to zoologists, and since it comes in the same category as Gazella (q.v.), we have adhered to the better known name of Hippotragus.

Remarks.-So far as one is able to judge from the scanty fossil material this genus has a relatively long geological history. Killgus (1922, p. 255) has described $H$. sinensis from the Lower Pliocene of China, and Lydekker (1886, p. 10) H. sivalensis from the Indian Pliocene. Both these species are very close to the African forms of the present day in skull characters. The chief differences are in the teeth, which are brachyodont with weak basal pillars in the fossils, and, in $H$. sinensis, the horn-cores are sub-triangular in cross-section as compared with the broad ellipse displayed by all the other species.

## Hippotragus kopassii Andree.

1926. Hippotragus kopassii Andree, Palaeontographica, LXVII, p. 158, pl. xv, figs. 8, го.

Diagnosis.-A Hippotragus with the horn-cores placed obliquely over the orbits, cross-section of horn-cores markedly elongate-elliptical. Orbits large, round, situated more than half their diameter in front of the horn-cores. Ethmoidal fossa slit-like and long; Lachrymal fossa very shallow.

Holotype. - The skull figured by Andree (1926, pl. xv, figs. 8, io). It is preserved in the Geological Institute at Münster.

Locality.-The type locality is Samos. None other is known.
Remarks.-This species agrees very closely with the modern forms in most particulars. The chief differences are the somewhat shorter brain-case, the more slender horns, and the more primitive teeth.

## Specimen.

M I3I66. Plaster cast of skull with the lower part of the horn-cores. The original is the holotype (Andree, 1926, p. 158, pl. xv, figs. 8, 10). Samos. By exchange with the Geological Institute, Münster, 1926.

## Genus PALAEORYX Gaudry.

186r. C. R. Acad. Sci. Paris, LII, p. 24 I .
Diagnosis.-Hippotraginae of large size, with broad, rather low skull, and short brain-case, face moderately bent down on the basicranial axis; lachrymal fossa shallow, or of medium depth ; supra-orbital foramina not sunken in depressions; horn-cores long, strongly tilted backward, curved slightly as a rule, though strongly in one species, more or less divergent, but with the tips generally converging to a greater or less extent, with cross-section round or elliptical, compression generally lateral but occasionally antero-posterior, without a keel; dentition moderately hypsodont, premolar series moderately short, $P^{2}$ of simple structure, basal pillars of molars present or absent, ribs generally strong.

Genotype.-Antilope pallasii Wagner (1857, p. I49).
Species.--Since it was established by Gaudry for the species from Pikermi described by Wagner as Antilope pallasii many other forms have been referred to

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this genus. Among those of which the characters agree more or less closely with those of the type may be mentioned P. majori Schlosser, P. laticeps Andree, and $P$. meneghinii Rütimeyer. $P$. ingens Schlosser is only known from the dentition. The form mentioned by Major under the nomen nudum P. rotundicornis appears to be indistinguishable from $P$. pallasii. We have referred $P$. parvidens Gaudry to the genus Microtragus Andree, to which genus P. stützeli Schlosser may also belong although it is not sufficiently known for this to be certain.

In the Middle Pliocene of France and Italy occur several ruminants which have been assigned to Palaeoryx by Depéret and Schlosser. These are P. boodon Gervais, $P$. cordieri Christol, P. recticornis de Serres, P. massoni Major. The most recent discussion of their affinities is by del Campana (1918) who definitely refers to a variety of Leptobos etruscus certain specimens from the lignites of Casino which Major and Pantanelli attributed to Palaeoryx cordieri. In our opinion, not only the specimens from Casino but also the fine skulls which are preserved in the Paris Museum as P.boodon, and P. cordieri are of the Leptobos type. Quite apart from the skull-characters, clearly shown by the specimens in Paris, the presence of distinct keels on the horn-cores of "Palaeoryx" boodon and "Palaeoryx" cordieri is quite sufficient to separate them from the true Palaeoryx. Of the two species $P$. recticomis and $P$. massoni the former is synonymous with $P$. cordieri, and the latter is insufficiently known. The horn-cores of the holotype of $P$. massoni have never been figured, and we are unable to determine its generic position.

In addition to the species mentioned above, a new species, based on a skull from Pikermi in the British Museum, and a variety of that species, based on a skull from Samos in the Lausanne Museum, are described below under the names $P$. roodreardi and var. columnatus.

Skull.--The horn-cores are distinguished by the fact that they slope backward in the plane of the face, by their slight curvature, and by their cross-section which varies from elliptical to circular. The degree of divergence differs considerably as between the species, and also, though not to the same extent, as between individuals.

In comparison with the length of the face, the brain-case is short and broad. Breadth is also a feature of the frontal region. When held with the basicranial axis horizontal the skull roof, which is of a gently curved profile, is also horizontal, and the occipital slopes away rearwards so that the condyles lie behind the occipital crest.

The orbits are not very large and their rims do not project to any great extent. The lachrymal fossa is extensive and fairly deep. Towards it there runs from the supra-orbital foramen a shallow groove. The position of the infra-orbital foramen varies slightly but it is usually in the region of $P^{2}$ and $P^{3}$. The tympanic bulla is rather small, wedge-shaped, and not inflated.

Dentition.-The premolar series is fairly short and the teeth are of simple structure. The molar teeth are only moderately hypsodont, and the basal pillars when present are not usually very strong. On the other hand, the external ribs are always well developed.

## Palaeoryx pallasii (Wagner).

1857. Antilope pallasii Wagner, Abh. Bayer. Akad. Wiss. München, VIII, p. I49, pl. vii, fig. 2 r.

I865. Palaeoryx pallasii Gaudry, Anim. Foss. Attique, p. 271, pl. xlvii, figs. I-5.
1894. Palaeoryx rotundicornis Major, nom. nud., Gisement Ossif. Mitylini, p. 24, No. 200.

Diagnosis.-A Palaeoryx with oval orbits almost wholly in front of the horncores, which diverge at an approximate angle of $40^{\circ}-45^{\circ}$; the tips of the horn-cores turned slightly inward.

Lectotype.-The skull and horn-cores figured by Wagner (1857, pl. vii, fig. 21). It is preserved in the Palaeontological Museum at Munich.

Localities.-The type locality is Pikermi.
This species is also known from Samos (Andree, I926, p. I60). Under the name "Palaeoryx taille de pallasii" an antelope has been recorded from Portugal, Barreira das Pombas, near Villa Nova da Rainha (Roman, igo7, p. 65).

Remarks.-Examination of the skulls preserved in London and Paris discloses a considerable range of variation in the cross-section of the horn-cores. As may be seen from the measurements given below the cross-section varies between elliptical and sub-circular. In the case of one frontlet in the British Museum (M II4I8) the transverse diameter of the horn-core actually exceeds the sagittal by 24 per cent., but, since the face, teeth and brain-case are lost, and it is possible that this specimen is not correctly identified, we do not wish to lay too much stress on this one instance. Apart from the horn-cores there is no reason for placing the skulls in more than one species, and, as is well known, the cross-section of the antelope horn-core is always variable within the limits of the species.

A skull preserved in the Museum at Lausanne (Cat. No. 200) was referred by Major to a species which he distinguished by the nomen nudum of Palaeoryx rotundicornis. It does not differ in any of its characters from $P$. pallasii. There is, in the British Museum, a skull from Pikermi (M II426) of which the brain-case is complete and which still retains the right horn-core. The cross-section of this horn exactly reproduces that of the specimen in Lausanne, although the horn itself is shorter and rather more curved. Further comparison is not possible because the entire face has been lost.

The dimensions in millimetres of the cross-section of the horn-cores of certain specimens are given in the following table :-

|  |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Sagittal diameter | 63 | 71 | 69 | 62 | 50 | 63 | 63 | 66 | 69 | 62 |
| Transverse diameter | 57 | 59 | 55 | 61 | 62 | 53 | 58 | 53 | 52 | 45 |
| Transverse diameter expressed as a percentage of the sagittal | 9 r | 83 | 80 | 98 | 124 | 84 | 92 | 80 | 75 | 73 |

Of these specimens the first seven are of $P$. pallasii; the next of $P$. majori; the next (Lausanne, 199) of $P$. woodwardi var. columnatus, and the last of $P$. woodwardi.

## List of Specimens.

Note.-All are from Pikermi, Woodward Colln.
M ro83i. Skull fairly perfect except for the loss of the upper third of both horn-cores and damage to the basicranial region; cheek dentition in a medium stage of wear.
MII.426. Skull fairly perfect as to the brain-case but lacking the frontal and facial regions, with only the left horn-core preserved.
M ro834. Frontlet.
Mir4I8. Frontlet of an individual with extremely broad horn-cores.
M II429. Fragmentary left maxilla with $M^{1-3}$.
M 12998 . Last upper molar in an early stage of wear.
M I3000. Right maxilla with complete cheek dentition in a medium stage of wear.
M r3oor. Right $d m^{4}$ and $M^{1}$ in an early stage of wear.
M I2997. Part of a left mandibular ramus with $P^{3}$ broken, $P^{4}$ in process of eruption, and $M^{1-2}$ in wear ; possibly associated with the preceding specimen.

## Palaeoryx laticeps Andree.

1926. Palacoryx laticeps Andree, Palacontographica, LXVII, p. r6I, pl. xiii, figs. 4, 4a, 6.

Diagnosis.-A Palacoryx with short, low, broad brain-case ; occipital condyles widely separated; frontal and fronto-parietal sutures only slightly thickened; orbits half in front of the horn-cores, relatively fairly large, oval. Horn-cores widely separated at the base ; circular in cross-section at the tips, sub-circular at the base ; divergence considerable ; curvature fairly great, turning inward at the tips.

Holotype.-The skull figured by Andree (1926, pl. xiii, figs. 4, $4^{a, 6)}$. It is preserved in the Geological Institute at Münster.

Locality.-The type locality is Samos. None other is known.
Remarks.-Among the specimens from Samos preserved in the British Museum there is only one (M 4I97) which is at all likely to belong to this species. This specimen, a frontlet with horn-cores, is so crushed from above that one cannot be certain of the skull-profile, or of the cross-section of the horn-cores. It approaches Andree's species in the breadth at the orbits, the flat frontal, and in the much tilted, strongly divergent horn-cores. The horn-cores stand farther apart at the base than they do in $P$. majori Schlosser, the distance is 36 mm . compared with 29 mm . in the holotype of the latter. They are too crushed for the cross-section to be determined.

## Specimen.

M 4197. A very much crushed frontlet with the lower thirds of the horns. Samos. Major Colln.

## Palaeoryx woodwardi n. sp.

(Pl. VI, figs. $\mathrm{I} a-\mathrm{I} d$; Pl. VIII, figs. $\mathrm{r}, \mathrm{r} a$.)
Diagnosis.-A Palaeoryx which differs from $P$. pallasii in the narrow horncores which, together with the frontal, are smaller relatively to the rest of the skull ; horn-cores more divergent ; orbits more circular and not so far forward; upper molars with weaker external ribs and without basal pillars.

Holotype.-A skull in the British Museum, regd. No. M 10832.
Locality.-The type locality is Pikermi. None other is known.
Remarks.-The species agrees with $P$. pallasii in the position of the horns, which slope backward in the plane of the face; in their trifling degree of curvature; in the breadth of the skull, especially in the occipital region; and in the short braincase. It differs from that species in the narrow horn-cores, a condition precisely comparable to that which obtains in Protoryx; in the smaller size of the horns and of the frontal relatively to the other dimensions of the skull ; in the greater degree of divergence of the horn-cores; in the more circular outline and more backward position of the orbit ; in the very much weaker external ribs of the upper molars, and the fact that these teeth are entirely devoid of basal pillars; in the more regular outline of the internal wall of $P^{2}$ and $P^{3}$, with very little trace of indentation.

There seems very little doubt that the species is more nearly allied to $P$. majori Schlosser from Samos. It agrees with the latter in the narrow, divergent horns; in the smaller breadth of the skull at the frontals ; in the relatively spacious brain-case ; and in the backward position and circular outline of the orbits. There are, however, marked differences between the two species. The horn-cores are considerably more tilted backward in P. woodwardi than they are in P. majori. The horn-cores of the latter species diverge more than they do in $P$. woodwardi, and the tips
converge strongly, whereas in $P$. woodwardi the inward curvature of the tips is only slight, a condition also found in $P$. pallasii (cf. Gaudry, I865, pl. xlvii, fig. I). Schlosser, in the dentition which he refers to $P$. majori, mentions the presence of weak basal pillars in $M^{2}$ and $M^{3}$, the external ribs of which appear to be as strong as they are in $P$. pallasii. This is the opposite of the conditions in $P$. woodwardi. The premolar series of $P$. majori is much shorter than that of $P$. woodwardi and the inner wall of $P^{2-3}$ is deeply indented.

The present species appears to share a smaller number of characters with $P$. laticeps. The main differences between the two species are that the horn-cores are not so strongly curved in $P$. woodwardi and do not stand so far apart on the frontals; they have not the same pronounced inward curve throughout their upper half ; their cross-section is roundly elliptical and not circular ; the orbits are not very far forward ; the width at the frontals is not so great.

## List of Specimens.

Note.-All these are from Pikermi, Woodward Colln.
M Io832. The holotype, a skull wanting only the tips of the horn-cores and the premaxillary region; cheek dentition in an advanced stage of wear. (Pl. VI, figs. $1 a-\mathrm{I} d$.)
The following specimens are provisionally referred to this species.
M I3002. Left mandibular ramus of an immature individual lacking $P^{2} ; P^{3}$ and $M^{3}$ almost unworn ; $P^{4}$ just erupting. (Pl. VIII, figs. I-Ia.)
M I3003. Right mandibular ramus lacking $M^{3}$; teeth in a medium stage of wear.

Palaeoryx woodwardi var. columnatus nov.
(Pl. V, figs. $\mathrm{I}, \mathrm{I} a$.)
1894. Palaeoryx pallasii Major, Gisement Ossif. Mitylini, p. 24, no. 199.

Diagnosis.-A Palaeoryx resembling $P$. woodwardi except in the greater divergence of the horn-cores ; in all upper molars having basal pillars, those of $M^{2}$ and $M^{3}$ being stronger, and in having stronger external ribs; in the shorter premolar series; in the enamel of $P^{2}$ showing a slight re-entrant fold absent from $P^{3}$.

Holotype.-A skull from Samos in the Major Collection at the Lausanne Museum, Cat. No. I99.

Locality.-The type locality is Samos. The variety may occur at Pikermi.
Remarks.-The holotype, which has the face badly preserved, but which retains one almost complete horn-core and the entire cheek dentition, was referred by Major to Palaeoryx pallasii. Its extremely narrow and widely divergent horn-cores militate against this reference, and invite comparison with either $P$. majori or $P$. woodwardi. It resembles the latter, rather than the former, in the slight inward curve and strong backward tilt of the horn-cores. The premolar series is intermediate
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in length between the two species. On the whole, in spite of the stronger ribs and basal pillars, we incline to refer this skull from Samos to the Pikermi species $P$. woodwardi, regarding it as a variety on account of the differences mentioned in the diagnosis.

A large palate in the British Museum (Mil4I6. Pl. V, figs. I, Ia) forms part of the Woodward collection from Pikermi. It belongs to an immature individual ; the last two milk molars are still in place, $P^{2}$ and $P^{3}$ are almost untouched by wear, and the crowns of $M^{1}$ and $M^{2}$ are only slightly worn. The united length of the molars is 75 mm . and that of the premolars 56 mm . ; the width of the palate between the last molars is 60 mm . The height of the crown of $M^{3}$ is 27 mm . Short basal pillars are present in all the molars, but the external ribs, especially in the middle of each lobe, are less strongly developed than in Palacoryx pallasii. A re-entrant fold is well seen in $P^{2}$, but is absent in $P^{3}$. The comparatively high degree of hypsodonty and the weaker development of the ribs entirely preclude a reference to $P$. pallasii, and on the other hand, the breadth of the palate is far too great for Protoryx carolinae. Moreover, if the crowns of the teeth of the varietal holotype were as high as this there would be no objection to placing the two specimens together. Since the dentition of the Lausanne specimen is in a fairly advanced stage of wear, as is also that of the holotype of $P$. woodwardi, it would not be safe to deny the possibility that, when unworn, the teeth of either specimen were not equally high. In the circumstances the Pikermi palate may be placed here.

It is remarkable that a palate, almost exactly like that just described, except that it belongs to an older individual, is in the collection made by Gaudry at Pikermi and now in the Paris Museum. De Mecquenem has figured a very similar palate from Maragha under the name of $P$. pallasii ( $1925, \mathrm{pl} . \mathrm{v}$, fig. 2). Another palate from Pikermi, preserved in the Munich Museum, agrees very well with the three specimens just mentioned.

## List of Specimens.

M 4205. Palate with $P^{3}-M^{2}$. The breadth between the last molars, 65 mm ., and the size of the premolars suggest that the specimen should be placed here despite the very faint indication of basal pillars in the molars. Samos. Major Colln.
M II4I6. Palate of a large inımature individual with $d m^{3-4}$ in place, $P^{2}$ unworn, and $M^{1-3}$ in an early stage of wear. (Pl. V, figs. I, Ia.) Pikermi. Woodward Colln.

## Palaeoryx ingens Schlosser.

1904. Palaeoryx ingens Schlosser, Beitr. Paläont. Geol. Oest.-Ung., XVII, p. 43, pl. viii, figs. 3-5.

Diagnosis.-A Palaeoryx of large size in which the teeth bear a close resemblance to those of $P$. pallasii but have more angular crescents.

Syntypes.-The teeth described and figured by Schlosser (1904, pl. viii, figs. 3, 4, 5). They are preserved in the Palaeontological Museum at Munich.

Locality.-The type locality is Samos. None other is known.
Remarks.-This species is unknown except from the isolated dentitions described by Schlosser. Up to the present it has not been recorded from any locality other than Samos. The skull and horn-cores are unknown.

## Palaeoryx majori Schlosser.

1904. Palaeoryx majori Schlosser, Beitr. Paläont. Geol. Oest.-Ung., XVII, p. 38, pl. vii, figs. 1-5.

Diagnosis.-A Palaeoryx with the orbits almost entirely beneath the horncores. Horn-cores broadly ovate in cross-section, the long diameter oblique to the antero-posterior axis of the skull, widely divergent, tips turning slightly inward.

Lectotype.-The frontlet figured by Schlosser (1904, pl. vii, figs. $5^{a,} 5^{b}$ ) is hereby chosen as the holotype of the species.

Locality.-The type locality is Samos. None other is known.
The species is also recorded from Rumania, Taraklia, Bendery (Khomenko, 1913, p. 126) and from the Ukraine, Toudorovo, Kherson (Pavlow, I914, p. 182).

Remarks.-This species differs from $P$. pallasii in having smaller and more primitive teeth, round orbits, not ovate, a larger brain-case, and straighter, more divergent, horn-cores the tips of which are more incurved.

## Palaeoryx? boodon Gervais.

1853. Antilope boodon Gervais, Bull. Soc. Géol. France, 2, X, p. 158, pl. v, figs. 1-9.

This species was described by Gervais from some teeth sent him from the lignite of Alcoy, Spain. As pointed out above, the skull in the Paris Museum labelled P. boodon is of the Leptobos type. It appears, however, that the deposits at Alcoy may be of the same age as those on Samos (Schlosser, 1904, p. 44). So far as we are aware Leptobos does not occur in the Pontian. There is, however, a genus Proleptobos which was established by Pilgrim (1913, p. 304) on a skull named by him Proleptobos birmanicus. The skull (Miogo9 B. M. G. D.) was found in Burma, in deposits which are probably of Pontian age. For this reason we think that the reference of skulls of that type to the species Antilope? boodon is not justifiable, and, further, that the species itself is at present indeterminate.

## Genus TRAGOREAS Schlosser.

1904. Beitr. Paläont. Geol. Oest.-Ung., XVII, p. 34.

Diagnosis.-Hippotraginae of medium size, with long, slightly curved, almost parallel horn-cores, inclined strongly backward, and of elliptical cross-section ; keels absent. Face moderately bent down on basicranial axis ; lachrymal fossa shallow; no ethmoidal vacuity. Upper dentition practically brachyodont, premolars primitive and but little differentiated.

Genotype.--Tragoreas oryxoides Schlosser (1904, p. 34).
Species.-Only two species of Tragoreas are known, the genotype and another described by Schlosser (1904, p. 35) as Tragoreas sp.

## Tragoreas oryxoides Schlosser.

1904. Tragores oryxoides Schlosser, Beitr. Paläont. Geol. Oest.-Ung., XVII, p. 34, pl. vi, figs. I, 6-9.

Diagnosis.-A Tragoreas with sub-parallel, keelless horn-cores of broadly elliptical cross-section. Lachrymal fossae not very deep but comparatively long. Orbits obliquely ovate, less than half under the horn-cores. Frontal and frontoparietal sutures slightly thickened.

Lectotype.-The skull figured by Schlosser (1904, pl. vi, figs. I, 9) is hereby chosen as the holotype. It is preserved in the Palaeontological Museum at Munich.

Localities.-In addition to the type locality of Samos this species has also been recorded from Rumania, Taraklia, Bendery (Khomenko, 1913, p. 127).

Remarks.-The crowns of the molars are low and are almost square in outline with comparatively stout ribs. The premolars are very primitive and differ but little from those of the Cervidae.

## Tragoreas? sp. Schlosser.

1904. Tragoreas? sp. Schlosser, Beitr. Paläont. Geol. Oest.-Ung., XVII, p. 37, pl. vi, figs. Io, II.

Remarks.-Under this heading Schlosser describes some lower jaws and teeth and a fragment of an upper jaw. The identification of the former is uncertain because the lower dentition of $T$. oryxoides is not definitely known ; the lower teeth so named by Schlosser were not found attached to the skulls on which the species was founded. Even more uncertain is the identification of the fragment of upper jaw. Apparently there is only one tooth, $M^{2}$, and this differs from those of true Tragoreas in several important details.

## Subfamily CERVICAPRINAE.

Diagnosis.-"Skull moderately long, slightly arched, with ethmoidal vacuity, without lachrymal fossa. Horns rather short, slightly inclined, lyre-shaped. Teeth hypsodont, bovine." (Schlosser, 1925.)

## Genus PROCOBUS Khomenko.

1913. Annu. Géol. Min. Russie, XV, livr. 4-6, p. 127.

This genus, with its two species $P$. melania and $P$. brauneri was described in Russian. For some reason the author limited his French summary to an account of some Cervidae, and to his conclusions, thereby omitting all mention of the new species of antelopes which he described. A certain amount of assistance is to be obtained from the figures which accompany his paper; the following remarks are based on them.

Genotype.-As genotype is selected Procobus melania, the first of the two species taken in the order in which they are described.

Procobus melania Khomenko.
1913. Procobus melania Khomenko, Annu. Géol. Min. Russie, XV, livr. 4-6, p. 127, pl. viii, fig. 18.

Holotype.-The frontlet figured by Khomenko (1913, pl. viii, fig. I8). It is preserved in the Geological Cabinet at Odessa.

Locality.-Taraklia, Bendery, Rumania.
Remarks.-This species is founded on a frontlet with two complete horncores. From the figure the horn-cores appear to be practically straight, divergent at an angle of approximately $30^{\circ}$, sub-circular in cross-section at the base, becoming circular as the tip is approached. The left horn-core, which preserves the tip, is 325 mm . in length. The profile is not figured.

## Procobus brauneri Khomenko.

1913. Procobus brauneri Khomenko, Annu. Géol. Min. Russie, XV, livr. 4-6, p. 128, pl. ix, figs. I, 2.

Holotype.-An imperfect skull retaining the lower half of the horn-cores and part of the palate, but lacking the brain-case, figured by Khomenko (19r3, pl. ix, figs. I, 2). It is preserved in the Geological Cabinet at Odessa.

Locality.-Taraklia, Bendery, Rumania.
Remarks.-The horn-cores diverge at an angle of some $40^{\circ}$ to $45^{\circ}$. From the figure it is not possible to learn anything about the face.

The upper molars are only very slightly hypsodont. They are square, devoid of basal pillars, have ribs of moderate strength, the inner crescents well rounded, and the outer ones showing some resemblance to a bovine type.

It is most unfortunate that these species were not published in a language which is generally understood by men of science. That the two forms are of some interest is evident from the figures, and it is a pity that full particulars have not been given in the French summary.

## Subfamily TRAGELAPHINAE.

Diagnosis.--" Skull long, slightly arched, with ethmoidal vacuity, in the fossil forms with lachrymal fossa also. Horns long, lyre-shaped, keeled and spiral, roundish in cross-section. Teeth always brachyodont, only in fossil forms with weak basal pillar." (Schlosser, 1925.)

Remarks.-In addition to the recent genera Tragelaphus, Strepsiceros, and Taurotragus there have been included in this subfamily the extinct genera Protragelaphus, Prostrepsiceros, Palaeoreas, and Helicotragus. We have already given our reasons for removing the last-named genus to the Gazellinae. The history of the forms which have been referred to one or other of the remaining fossil genera may now be shortly summarized.

Palaeoreas was founded by Gaudry (r86r, p. 299) with Antilope lindermayeri Wagner as genotype. This species has horn-cores which are twisted in a close spiral,
somewhat after the manner of Taurotragus, and which are provided with two strong keels. The face is bent at a right angle to the basicranial axis. This is an important point of difference from the recent forms. The species P. montis-caroli Major, an Italian species, and P. gaudryi Thomas from Algiers have been discussed by Weithofer (1889, p. 78), Schlosser (1904, pp. 78, 80), and del Campana (1918, p. 220). They are both of uncertain affinity, are imperfectly known, and need not be considered further.

Rütimeyer (1877-8, pp. 84-85) and Depéret (1883-4, p. 278) have remarked on the resemblance to both Palaeoreas and Strepsiceros of an antelope from the Upper Pliocene, or Lower Pleistocene, of Auvergne which they refer to Antilope torticornis Aymard. Schlosser (1904, p. 78) seems to accept this, and definitely to regard the species as a Palaeoreas. The species A.torticomis was never described by Aymard, who only gave a small uncharacteristic figure of a single horn-core. It is not at all well known, and the original material needs revision. The very fine skull in the Paris Museum is certainly not $A$. torticornis as interpreted by Rütimeyer and Depéret. Both authors mention the presence of two keels on the horn-cores, whereas the skull in question has a strong posterior keel, as in Protragelaphus skouzési, but no anterior keel. Indeed, it approaches more closely to $P$. skouzési than to any other species.

Dames (1883, p. 95) gave the name Protragelaphus skouzèsi to a skull from Pikermi with horn-cores which form a more open spiral than those of Palaeoreas lindermayeri, and which have only one strong keel arising from the postero-external part of the base. He pointed out that one of the skulls referred by Wagner (I857, p. 155, pl. vii, fig. 18) to Antilope lindermayeri really belonged to this species. Weithofer (1888, p. 285) wrote a detailed description of this species and figured another specimen, also from Pikermi. The same species was recognized by Rodler and Weithofer (1890, p. 769) at Maragha and again by de Mecquenem in the same locality. In neither case did the specimens differ appreciably from the type.

Rodler and Weithofer ( 1890, p. 768) described and figured another antelope from Maragha which they named Tragelaphus? houtum-schlindleri. This species possessed not only the posterior keel of Protragelaphus skouzèsi but also a strong anterior keel, the cross-section of the horn-core being distinctly flattened on one side between the two keels. Forsyth Major (1891, p. 609) made this species the genotype of Prostrepsiceros to which genus he also referred some specimens from Samos under the names Prostrepsiceros woodwardi and Prostrepsiceros? sp. These were never described or figured, but there is little doubt that the specimens are those preserved in the British Museum numbered M4192 and M4210. The better of the two specimens ( M 4192 ) is a skull, perfectly preserved as to the horn-cores, but defective as to the face and brain-case. It is the holotype of $P$. woodwardi (q.v.). The more fragmentary one ( $\mathrm{M}_{4}$ 210) is a frontlet with about 40 mm . of the horn-cores attached. This seems to agree exactly with Hemistrepsiceros zitteli (Schlosser) and cannot be separated from that species. In his collection from Maragha de Mecquenem (1925) had several horn-cores and fragmentary skulls which he identified as Tragelaphus houtum-schlindleri, and of which he figured one skull. Below (p. 92) we give
reasons in support of our opinion that these are not identical with the holotype of $P$. houtum-schlindleri and should be placed in another species.

Descriptions and figures of another Samos specimen, to which Schlosser gave the name Protragelaphus zitteli, are contained in that author's monograph "Die fossilen Cavicornia von Samos" (1904, p. 31). References to skulls of P. skouzèsi and $P$. zitteli described by Andree, and to another skull in the Münster collection, referred by Andree to Tragelaphus? sp., complete the record of published work on the fossil remains referred to these various genera.

Coming now to the classification of these species, it is evident, as Major and Schlosser realised, that the species $P$. houtum-schlindleri differs from either of the recent genera Tragelaphus or Strepsiceros by reason of the greater bending down of the face on the basicranial axis, by the presence of a deep lachrymal fossa, and by the more brachyodont teeth. In the latest (1923) edition of Zittel, " Grundzüge der Paläontologie," the distinction between Protragelaphus and Prostrepsiceros is based on the presence of one or two keels to the horn-cores. This distinction is satisfactory if only the species Prostrepsiceros houtum-schlindleri and Protragelaphus skouzèsi are considered; with additional species in each genus difficulties arise. In the first place, however, it is difficult to deny the existence of a second keel in Prostrepsiceros woodwardi, seeing that, for the greater portion of the length of the horn, such a keel is plainly present; in the second place, although $P$. skouzési and $P$. zitteli each possess a single keel, yet the position of that keel is exactly opposite in the two species.

In the modern genera the distinction is based, not on the existence of a second keel, but on the presence of a strong posterior keel in Tragelaphus, even though such a keel is present in some degree in Strepsiceros imberbis, and of a strong anterior keel in Strepsiceros. It seems likely that these keels in their present position existed in the ancestors of each particular form, while the horns were yet straight and had not begun to twist. This may be inferred from the fact that in the young males of each of the modern species the horns start straight, and only gradually assume a spiral form. But even in these young animals the characteristic keels are quite as well marked as they are in the adult. It seems therefore impossible to suppose that a keel evolved in this group at a later period than the Pontian ; the different lines had already become fully differentiated, and only variations in the degree of torsion may be expected to have taken place since. If this be true it follows that any classification based on phylogenetic considerations must take into account the presence or absence of each keel, since this character appears to be constant and important, and only discordance with other characters of greater importance would justify us in disregarding it.

We are, therefore, faced with two alternatives. We may either unite the four fossil species in one genus, as some authors (Lydekker \& Blaine, I9I4, Catalogue of the Ungulate Mammals in the British Museum, III, p. I94) are in favour of doing in the case of the recent genera Strepsiceros and Tragelaphus, or, by recognizing the fact that the single keel of $P$. zitteli and $P$. skouzési is situated on opposite sides of the horn-core, separate these two species generically. The former alternative is
contrary to the procedure which generally finds favour to-day, and would involve difficulties concerning Palaeoreas. Consequently the latter is adopted here and $P$. zitteli is separated under the generic name Hemistrepsiceros. The four genera are diagnosed below in the appropriate places.

## Genus PALAEOREAS Gaudry.

1861. C. R. Acad. Sci. Paris, LII, p. 299.

Diagnosis.-Small Tragelaphinae with short face and brain-case; face bent down on basicranial axis almost to a right angle ; lachrymal fossa deep ; supra-orbital foramina large and sunken; horn-cores large, strongly tilted backward, straight, moderately divergent, spirally twisted, forming a close spiral of about two revolutions, with an approximately circular cross-section, having two distinct keels, one anterior and one posterior ; dentition moderately hypsodont, with premolar series of medium length, basal pillars generally present but sometimes absent, ribs weak, premolars moderately complicated.

Genotype.-Antilope lindermayeri Wagner, 1848.
Species.-Other species which have been referred to this genus are mentioned above (p. 84). The remains are fragmentary and do not permit of certain generic determination.

## Palaeoreas lindermayeri Wagner.

1848. Antilope lindermayeri Wagner, Abh. Bayer. Akad. Wiss., V, p. 367, pl. xii, figs. 2-5.
1849. Palaeoreas lindermayeri Gaudry, Anim. Foss. Attique, p. 2go, pl. lii, fig. 4 ; pl. liii, figs. I-3; pl. liv; pl.lv.
Diagnosis.-The only undoubted Palaeoreas. The specific characters are those of the genus.

Holotype.-The broken horn-core figured by Wagner (1848, pl. xii, fig. 5). It is preserved in the Palaeontological Museum at Munich.

Localities.-The type locality is Pikermi. The species also occurs at Samos.
The tip of a horn-core is recorded from Macedonia, Veles (Schlosser, 192I, p. 44).
Remarks.-In the Woodward collection from Pikermi there is a skull of this species (M 10843) which is fairly perfect in the frontal and facial regions; it has the complete cheek dentition in a moderately advanced stage of wear, but lacks the hinder part of the skull. There are several frontlets in the collection and a few isolated horn-cores. A number of isolated maxillae and mandibular rami may be referred with very little hesitation to this species. As observed above (p. 19), the dentition of Helicotragus is at present unknown, but it is extremely likely that the teeth are similar in size to those of this species; in these circumstances one cannot exclude the risk that the dentition of the two species may have been confused, especially in the case that their structure should happen to be almost identical.

The skull in the British Museum is slightly smaller than the one figured by

Gaudry, and the frontal suture is considerably swollen; otherwise no definite differences seem to exist.

The series of horn-cores vary somewhat in size, and in the rapidity with which they taper to the tip. The degree of prominence of the keel also varies; the anterior keel especially being, in some cases, feebly developed.

This species undoubtedly occurs at Samos. It is represented by three skulls in the Major collection at Lausanne (Cat. Nos. 23, 24, 25).

## List of Specimens.

Note.-All are from Pikermi. Woodward Colln., unless otherwise stated.
M 10843. Skull lacking the hinder part of the brain-case.
49712. Frontlet with the left horn-core. Purchased 1879.

M io84I. Frontlet with short horn-cores ; deep supra-orbital pits are shown.
M 10842 . Frontlet with short horn-cores.
M II432. Two frontlets with stout horn-cores tapering rapidly to the tips; both anterior and posterior keels of the horn-cores are pronounced.
M II433. Frontlet with horn-cores; posterior keel prominent, anterior keel faint at the base.
M ir434. Frontlet with horn-cores ; posterior keel less prominent than usual.
M ir 447. Three maxillae showing the complete cheek dentition in a medium stage of wear.
M гого. Left maxilla of an immature individual with $d m^{3-4}$ in an advanced state of wear, $M^{1-2}$ slightly worn, and $M^{3}$ just being cut.
49713. Fragment of the left mandibular ramus with $M_{1-3}$. Purchased 1879 .

MII448. Almost complete mandibular ramus of an immature individual. There was no $d m_{2}$, but the germ of $P_{2}$ has been exposed by chipping away the originally perfect edge of the jaw ; $d m_{3-4}$ still in wear, $M_{2}$ slightly worn, $M_{3}$ only partially erupted.
M 13007. Left mandibular ramus with the complete dentition, except $P_{2}$, in an early stage of wear.
M I3008. Left mandibular ramus with $P_{2-3}$ broken off, the remaining cheek teeth in a medium state of wear.

## Genus PROTRAGELAPHUS Dames.

1861. Palaeoreas Gaudry pars, C. R. Acad. Sci. Paris, LII, p. 24 r.
1862. Protragelaphus Dames, Sitzber. Ges. Naturf. Fr. Berlin, p. 97.

Diagnosis.-Tragelaphinae of medium size, with moderately short face and brain-case ; face bent down on basicranial axis at somewhat more than a right angle ; lachrymal fossa deep; supra-orbital foramina small and not sunken; horn-cores of medium size, rather widely divergent, tilted backward to a greater or less extent, forming a slightly open spiral of about two revolutions, with an approximately
circular cross-section, having a strong posterior keel but none anteriorly. Cheekteeth moderately hypsodont, with weak ribs, basal pillars absent; premolar series short, the teeth simple in structure.

Genotype.—Protragelaphus skouzési Dames.

# Protragelaphus skouzèsi Dames. 

(Pl. IX, figs. 2, 3.)
1857. Antilope lindermayeri Wagner pars, Abh. Bayer. Akad. Wiss., VII, p. 155, pl. vii, fig. 18.
1865. Palaeoreas lindermayeri Gaudry pars, Anim. Foss. Attique, pl. liii, fig. 4.
1883. Protragelaphus skouzèsi Dames, Sitzber. Ges. Naturf. Fr. Berlin, p. 97.

Diagnosis.-This is the genotype and only species. Its characters are those of the genus.

Holotype.-The specimen described, but not figured, by Dames (1883, p. 97). The specimen figured by Wagner ( 1857 , pl. vii, fig. I8) was referred to this species by Dames ; it may be taken as the paratype.

Localities.--The type locality is Pikermi.
The species is also recorded from Macedonia, Veles ( $P$. cf. skouzèsi Schlosser, 1921, p. 44) ; Rumania, Taraklia, Bendery (Khomenko, 1913, p. 127) ; Samos (Andree, 1926, p. 165, pl. xv, figs. 4, 5) ; Ukraine, Grebniki, Kherson (Pavlow, 1914, p. 182).

Remarks.-A skull from Pikermi (r0840) shows the frontal and occipital regions well, but lacks the maxillae and the teeth. It agrees remarkably well with a specimen, also from Pikermi, described and figured by Weithofer (1888, p. 285, pl. xvii, figs. 4-6), and also with the frontlet and horn-cores figured by Wagner of which there is a cast in the British Museum (M 4068). The horn-cores are smaller than in Weithofer's specimen, and the brain-case appears to be shorter. In Wagner's specimen the horn-cores are bigger but the occiput is equally short; in this skull the horn-cores stand closer together than in either of the two others.

The skull from Maragha figured by de Mecquenem (1925, p. 36, pl. v, fig. 2 ; pl. vi, figs. I, 6) is also referable to this species. It preserves the maxillary region with the teeth in a medium stage of wear.

A left maxilla in the Woodward collection retains $P^{4}-M^{3}$ (M II439; Pl. IX, figs. $2,2 a$ ) and agrees well with the corresponding region of the skull from Maragha. The teeth are much more hypsodont than in Palaeoryx, and the ribs of the external walls are not so strong. The molars are devoid of basal pillars, although in the skull figured by de Mecquenem (1915, pl. v, fig. 2) a slight basal pillar is present in $M^{1}$. Both $P^{4}$ and the molars have spurs of enamel which project into the central cavity ; $M^{1}$ shows an enamel island in the middle of the tooth. In the Maragha skull both $P^{2}$ and $P^{3}$ have a re-entrant fold in the enamel of the inner wall of the tooth. The dentition most nearly resembles that of Palaeoreas lindermayeri, but, apart from its greater size, the premolar series is relatively shorter than in that species.

Four fragments of mandibular rami in the Woodward collection may be referred to this species. Of these one (M 13022) is figured (Pl. IX, fig. 3). They
all agree in size and character with the specimen from Maragha figured by de Mecquenem ( $1925, \mathrm{pl}$. vi, fig. I), and also with that from Pikermi figured by Gaudry (r865, pl. liii, fig. 4) under the name Palaeoreas lindermayeri, which, however, as de Mecquenem points out, is referable to Protragelaphus skouzèsi. The molars all have basal pillars ; the premolar series is relatively short, and the structure of the individual teeth is more simple than it is in Palaeoreas. Except for their greater size, these rami remind one more of the specimens provisionally referred above to Helicotragus (p. 23). The material under consideration does not add anything to the descriptions of Weithofer and de Mecquenem.

## List of Specimens.

Note.-All are from Pikermi. Unless otherwise stated they are Woodward Colln.

M 4068. Cast of skull figured by Wagner (1857, pl. vii, fig. I8). By Exchange I889.
M ro840. Skull, lacking maxillae and teeth.
M ir439. Left maxilla with $P^{4}-M^{3}$. (Pl. IX, figs. 2, 2a.)
M I302I. Right mandibular ramus with full cheek dentition, except $P_{2}$ which is only represented by its roots.
M 13022. Right mandibular ramus with $P_{2}-M_{3}$. (Pl. IX, fig. 3.)
M I3023. Right mandibular ramus with $M_{1}-M_{3}$.

## Genus PROSTREPSICEROS Major.

189ı. C. R. Acad. Sci. Paris, CXIII, p. 609.
Diagnosis.--Small Tragelaphinae with rather broad face, and short, slender brain-case ; face bent down on basicranial axis almost to a right angle, especially wide at the frontals; horn-cores large, moderately divergent, strongly tilted backward, forming an almost completely open spiral of from one-half to two revolutions, with a flattened cross-section, especially marked in the upper three-quarters of their length, having two keels, one anterior and one posterior; lachrymal fossa deep; supra-orbital foramina large and sunken ; orbits not situated in front of the horncores; dentition rather precociously hypsodont, with weak ribs, basal pillars absent in the molars, premolar series short, premolars of simple construction.

Genotype.-Tragelaphus? houtum-schlindleri Rodler \& Weithofer.
Species.--The history of this genus is related above (p. 84). We include in it the three species $P$. houtum-schlindleri Rodler and Weithofer, this is the genotype, the holotype being a skull from Maragha in the Vienna Museum, P. mecquenemi nov., of which the holotype is the skull from Maragha in the Paris Museum described by de Mecquenem as $P$. houtum-schlindleri, and the species $P$. woodwardi nov. The last appears as a nomen nudum in Major (18gI et seq.), but is now described and figured for the first time from a frontlet in the British Museum, collected in Samos, and assumed to be the specimen which Major had in mind.

Skull.-The horn-cores are placed over the orbits. They are distinctly flattened in the basal cross-section, and this flattening may increase as the tip of the horn is approached. There is an anterior as well as a posterior keel on the horn-cores, which are twisted in a fairly open spiral of from half to two revolutions; the anterior keel is usually the sharper.

The brain-case is apparently short and slender when compared with the rather broad face, but, since all the known specimens which are referable to this genus have the brain-case badly damaged, it is not possible to be certain as to its features.

The orbits are moderately large and have slightly projecting rims. The lachrymal fossa is large and very deep. The supra-orbital foramina are large and situated in depressions below the general level of the frontals.

Dentition.-There are no basal pillars present in the upper molars although they occur in the lower jaw (de Mecquenem, 1925, p. 38). The premolars are not so reduced relatively as they are in Protragelaphus skouzèsi and are of simple construction.

Remarks.-The genus Prostrepsiceros is of interest for the manner in which it differs from the recent genera also placed in the Tragelaphinae. Some of the more important of these differences are considered here.

The face is bent down on the basicranial axis at very nearly as much as a right angle, and so agrees with all the fossil genera of the subfamily, though Hemistrepsiceros has not preserved this character in any of the specimens yet discovered. This is a very marked distinction from the recent genera, especially from Tragelaphus and Strepsiceros, in which the angle between the facial and basicranial axes is always very obtuse. The fronto-parietal suture almost coincides with the hinder edge of the horn-cores in the fossils, and runs at right angles to the antero-posterior axis of the skull. In Tragelaphus and Strepsiceros, however, the same suture is from 20 mm . to 30 mm . behind the horn-cores in the median line and is directed forward from that point on either side. It is noteworthy that young individuals of these two recent genera show the same condition of the suture as the fossil genus, and that it only gradually takes up the position found in the adult as the horns increase in size. A further feature found in Prostrepsiceros, but absent in the recent genera, is a slight swelling of the same suture, which causes a depression between it and the horn-cores.

Both the lachrymal fossae and the supra-orbital foramina differ from those of the recent genera. In the genera Tragelaphus and Strepsiceros the former are absent, and the latter are smaller and not sunken.

The backward slope of the horn-cores in the plane of the face in Prostrepsiceros agrees with the condition found in Tragelaphus; in Strepsiceros they are more upright. The horn-cores are more divergent than they are in the recent genera of this subfamily.

There are several features of greater or less importance in which Prostrepsiceros approaches, or departs from, the other fossil Tragelaphine genera. It agrees with the other fossil members of the subfamily in having the face bent down on the basicranial axis at an angle which is very nearly a right angle, though Hemistrepsiceros is yet unknown in this respect. Agreement with Protragelaphus is seen in the very
deep lachrymal fossa, and a difference from that genus in the large, sunken supraorbital foramina. Again, the breadth of the forehead at the orbits is considerably greater than it is in Hemistrepsiceros, and the horn-cores are also larger than in that genus, both in regard to length and to stoutness. On the other hand, although the horn-cores of Prostrepsiceros are, proportionately, larger than they are in Protragelaphus they are not so divergent ; the angle of divergence in Prostrepsiceros and Hemistrepsiceros is roughly equal. In cross-section the horn-cores differ considerably from those of either of the two last-mentioned genera. The spiral of the horncores is closer in Protragelaphus and Hemistrepsiceros than it is in Prostrepsiceros; the former genus has no anterior keel, but an anterior keel is found in Hemistrepsiceros, which has not a posterior keel.

The molars agree quite well with those referred to Hemistrepsiceros by Schlosser, and in the degree of hypsodonty, and strength of the external ribs the genus Prostrepsiceros appears closely to resemble Protragelaphus.

## Prostrepsiceros woodwardi n. sp. ex Major nom. nud.

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\text { (Pl. VII, figs. } \mathrm{x}, \mathrm{x} a, \mathrm{r} b .)
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189r. Prostrepsiceros woodwardi Major, nom. nud., C. R. Acad. Sci. Paris, CXIII, p. 608.
Diagnosis.-A Prostrepsiceros with the horn-cores twisted through one revolution.

Holotype.-A skull and horn-cores in the Major collection in the British Museum. Regd. No. M 4192.

Locality.-The type locality is Samos. None other is known.
Remarks.-The holotype is almost complete in the frontal region, with the right horn-core entire and two-thirds of the left. The maxillae contain the three left molars, $M^{1}$ is much broken, and right $M^{3}$. A large part of the parietals is preserved but the occipital, basicranial and ear regions are lost.

The face is bent down on the basicranial axis at very nearly a right angle. In this it agrees with all the fossil species of the subfamily. De Mecquenem (I925, p. 38) observes that the angle is less open in the specimens which he referred to $P$. houtum-schlindleri (vide $P$. mecquenemi infra). The characters of the lachrymal fossa and of the supra-orbital foramina are the same in all three species of the genus.

The horn-cores are not so divergent as in $P$. houtum-schlindleri. Their bases are separated by an interval of about 23 mm . Their cross-section at the base is distinctly flattened : the sagittal and transverse diameters are 28 mm . and 37 mm . respectively. The genotype shows an equally flattened cross-section. In P. woodwardi the flattening becomes more marked higher up the horn, and the shape of the cross-section near the tip approaches that of $P$. houtum-schlindleri. The anterior face of the horn-core in the latter species appears to be more convex than it is in the former. A blunt, rounded keel ascends spirally from the antero-internal corner of the base. Such a keel is also present in the other two species of the genus. A second keel arises from the postero-external angle of the base in both $P$. houtumschlindleri and $P$. mecquenemi ; it extends from the base to the tip of the horn-core.

The corresponding keel in $P$. woodwardi is not very strong for the first 30 mm . of its course, but above that point it becomes increasingly prominent. In this respect the fossil species agrees with the recent Strepsiceros imberbis.

The occipital region is absent from the holotype, and is otherwise unknown.
The teeth are not preserved in the specimen of $P$. houtum-schlindleri figured by Rodler and Weithofer, but are shown in the holotype of $P$. mecquenemi from Maragha. A small island of enamel is formed in the centre of the tooth as wear proceeds, and small basal pillars are present. The molars of $P$. woodwardi are approximately the same size as those of $P$. mecquenemi, but in the latter species there are no basal pillars (de Mecquenem, 1925, p. 38).

In the flattening of the cross-section of the horn-cores, and in their rather open spiral, the species $P$. houtum-schlindleri, $P$. mecquenemi, and $P$. woodwardi agree more closely among themselves, than they do with any of the other species referable to this subfamily. At the same time $P$. woodwardi is readily distinguished from its congeners by the very slight development of the posterior keel at the base of the horn-core, by the more regularly elliptical cross-section, and by the smaller degree of divergence of the horn-cores, which contain a greater number of revolutions than those of the genotype and a less number than those of $P$. mecquenemi.

## List of Specimens.

Note.-Both are from Samos, Major Colln.
M 4192. Holotype. A skull showing the frontal region well, with the right horn-core quite perfect and half of the left horn-core ; maxillae incompletely preserved with the three molars on the left side, and the last molar on the right side in an advanced stage of wear ; occipital and basicranial regions lost. (Pl. VII, figs. I-Ib.)
M 4213. Portion of the right horn-core of a smaller individual than the holotype.

## Prostrepsiceros mecquenemi, n. sp.

1925. Tragelaphus houtum-schlindleri de Mecquenem, Ann. Paléont., XIV, p. 37, pl. v, figs. 5, 7 ; pl. vi, figs. 5, 7.
Diagnosis.-A Prostrepsiceros with the horn-cores twisted through from one and a half to two revolutions.

Holotype.-As holotype is chosen the skull figured by de Mecquenem (1925, pl. vi, fig. 7). It is in the Paris Museum.

Locality.-Maragha, Persia.
Remarks.-Although unknown from European deposits there can be no doubt that this is a convenient place to deal with this species, especially as we regard it as distinct from the other two.

There are some ten skulls and fragments which were studied through the kindness of Prof. Boule and Mr. de Mecquenem. They all agree remarkably well among themselves, and the holotype is typical of them all. Although, in the size and shape of the cross-section, the horn-cores do not differ appreciably
from those of the holotype of $P$. houtum-schlindleri (Rodler \& Weithofer, 1890, p. 768 , pl. vi, fig. 2), yet they are all twisted to a greater extent than they are in that species, the spiral consisting of one and a half to two revolutions, instead of half a revolution. De Mecquenem does not appear to have regarded this difference as important and assigned all the specimens to the older species. For our part we think that the greater torsion of the horn-cores in all the specimens in Paris must be of specific significance, unless, indeed, the Vienna specimen is immature. There is, however, no reason to suppose that such is the case ; accordingly we have thought it advisable to separate all de Mecquenem's specimens as a new species.

The measurements of this species, so far as they may be obtained, are given below. The greater part of the brain-case is missing in the holotype, but is well preserved in another of the specimens.

The particulars in which the skull of this species differs from that of Protragelaphus skouzési have been stated by de Mecquenem; the following are the more important: (I) the horn-cores are proportionately larger ; (2) the spiral twist is more open ; (3) an anterior keel is present ; (4) the cross-section is flattened and not circular ; (5) the face is more bent down on the basicranial axis ; (6) the supra-orbital foramina are large and sunken, instead of being level with the general surface of the frontals; (7) the occipital condyles lie much further to the rear, in consequence of which the occipital forms an extremely obtuse angle with the parietal.

In regard to the first six of these the agreement with $P$. houtum-schlindleri is close, and, since the brain-case is unknown in that species, it is not possible to make any comparisons in respect of 7 . P. mecquenemi agrees with $P$. woodwardi in 2 , $3,4,5,6$, and partially in I . With regard to 7 no comparison is possible. In $P$. mecquenemi, however, the horns are proportionately larger than in $P$. woodwardi, and their posterior keel is extraordinarily strong and sharp from the base up, whereas it is very faint at the base of the horn-cores of $P$. woodwardi. The spiral of the horn-cores makes from one and a half to two revolutions instead of the one found in $P$. woodwardi, and the horns diverge more than they do in that species; the angle of divergence is very little less than it is in Protragelaphus ; finally, whereas in $P$. woodwardi the cross-section of the horn-core is a regularly flattened ellipse, in $P$. mecquenemi one side is much more strongly convex than the other, in which it agrees with $P$. houtum-schlindleri.

De Mecquenem has described and figured both the upper and lower dentitions of this species; the latter from a mandible associated with the holotype. The premolar series is rather longer than it is in Protragelaphus skouzesi, and the external wall in the upper premolars is less simple than it is in that species.

## Dimensions:



## Genus HEMISTREPSICEROS nov.

1904. Protragelaphus pars, Schlosser, Beitr. Paläont. Geol. Oest.-Ung., XVII, p. 3r.

Diagnosis.-Small Tragelaphinae with moderately large horn-cores forming an open spiral of about two revolutions, standing rather far apart on the frontals, moderately divergent, circular in cross-section, with a strong anterior keel, but none posteriorly. Supra-orbital foramina large and sunken.

Genotype.-Protragelaphus zitteli Schlosser, Igo4.
Remarks.-This genus is only known from a few frontlets, and the details of the remainder of the skull, together with those of the dentition, have still to be ascertained.

At present the chief difference between Hemistrepsiceros and Protragelaphus lies in the fact that the single keel is anterior in the former and posterior in the latter.

## Hemistrepsiceros zitteli (Schlosser).

1904. Protragelaphus zitteli Schlosser, Beitr. Paläont. Geol. Oest.-Ung., XVII, p. 31, pl. vi, figs. 2, 3, 5, I2.

Diagnosis.-The only species, the characters are those of the genus.
Lectotype.-The frontlet and horn-cores figured by Schlosser (1904, pl. vi, fig. 5). It is preserved in the Palaeontological Museum at Munich.

Locality.-The type locality is Samos. None other is known.
Remarks.-The solitary specimen in the British Museum does not enable us to add anything to Schlosser's description.

The dentition is unknown. Schlosser describes and figures (1904, pl. vi, figs. 2, 3, 12) certain teeth which he tentatively assigns to this species, but there can be no certainty in the matter until a skull is discovered in which the teeth are preserved.

## Specimen.

M 42Io. A fragmentary frontlet; probably the specimen referred to by Major (189I, p. 608) under the name Prostrepsiceros? sp. Samos. Major Colln.

## Genus TRAGELAPHUS ?

Remaris.-Under this heading Andree (r926, p. r66, pl. xiii, fig. I, pl. xv, fig. 9) describes and figures a skull from Samos. We have not seen the specimen, which is preserved in the Geological Institute at Münster, but from the figures and description we feel sure that a reference to Tragelaphus is erroneous. The keel on the horn-cores is blunt and anterior. The keel in Tragelaphus is posterior. In Andree's specimen the hinder surface of the horn has a comparatively deep groove on the lower half of the hinder surface of the horn-core, a feature not found in Tragelaphus.

## DOUBTFUL SPECIMENS.

In addition to the specimens mentioned in the following lists there are numerous specimens of bones and teeth of antelopes from Pikermi in the Woodward collection. These are unregistered, and are, as a rule, too fragmentary for exact determination.

## i. Specimens from Samos. Major Coll.

M 42II. Skull of a medium-sized antelope, with a long and slender braincase ; face bent down at right angles to the basicranial axis; horn-cores relatively large, apparently elliptical in cross-section but too poorly preserved to show definite characters.
M 4186. Right mandibular ramus of a small antelope with $M_{1-3}$.
M 4187. Right mandibular ramus of a small antelope with $M_{1-3}$.
M 4I88. Lower incisors and premolar of a small antelope.
M 4198. Vertebra of a large antelope.
M 4339. Vertebra of a large antelope.
M 4346. Lumbar vertebra of a medium-sized antelope.
M 4189. Imperfect radius and ulna.

## ii. Specimens from Pikermi. Woodward Coll.

M iI486. Upper part of a horn-core, about 150 mm . in length, not twisted, narrow, elliptical cross-section, slight backward curvature, no torsion, slightly crushed.
M II477. Distal end of humerus of a medium-sized antelope.
M ir467. Carpals and metacarpals of a small antelope (Palaeoreas ?).
M II473. Short, stout metacarpus of a moderately large antelope.
M II474. Long, slender metacarpus of a moderately large antelope.
M in49I. Proximal end of a femur.
M II470. Distal end of tibia, tarsus, metatarsus and phalanges of a moderately large antelope (Tragocerus ?).
M II47I. Fragments of tibia, tarsus and part of metatarsus of a moderately large antelope (Tragocerus ?).
M II472. Distal end of tibia, tarsus and part of metatarsus of a moderately large antelope (Tragocerus?).
M II478. Left tibia of a moderately large antelope.
M II479. Right calcaneum of a medium-sized antelope.
M II475. Tarsus, metatarsus and phalanges of a large antelope, the bones are very stout.
MII476. Phalanges.
iii. Specimens from Concud. Unless otherwise stated all are Woodward Colln.

M 8309. Palate of a medium-sized antelope ; the premolars are fragmentary.
M 8306. Two upper molars of a medium-sized antelope.

M 8307. Two lower molars of a medium-sized antelope.
M roo95. Third lower molar of a moderately large antelope. Purchased 1906.

M 83ro. Scapula of a small antelope.
M roog8. Astragalus of a medium-sized antelope. Purchased. 1906.
M roog9. Calcaneum of a medium-sized antelope. Purchased. 1906.
M 8312. Tarsal of a small antelope.

## LIST OF WORKS CONSULTED

The works mentioned in the following list are those consulted in the preparation of this Catalogue. In every case the reference has been checked from the original. An attempt was made to see every paper in which the Pontian Bovidae of Europe were mentioned and it is believed that, with the exception of certain Russian publications which were unavailable, this has been achieved. While it is recognised that the list is not complete, it is hoped that it will furnish a guide to the somewhat scattered literature, and will indicate where other papers may be found. So far as possible the contractions are based on those in the World List of Scientific Literature.

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ATHANASIU, Sava. Igo7. Mamifère Terțiare din România. Anuar. Inst. Geol. Romaniei, I, pp. I2g2I4, pls. i-xii. (Rumanian. German summary.)
BENDA, LÁszLó. 1927. A Baltavári öslénytani ásatások 70 éves története 1856 -1g26. 80 pp .2 figs., small 8vo. Szombathely. (Hungarian. German summary.)
BLAINE. See LYDEKKER, R., \& BLAINE, G.
BORISSIAK, Alexis. 1g14. Mammifères Fossiles de Sebastopol. Mém. Com. Géol. St. Petersburg, N.S., Livr. 87, pp. xii, 154, pls. i-x. (Russian. French translation.)

BOULE, Marcellin. I8g6. Le Cantal Miocène. Bull. Serv. Carte. Géol. Fr., VIII, pp. 213-248, pl. i.
del CAMPANA, Domenico. Igi8. Considerazione sulle Antilopi Terziaire della Toscana. Palaeontogr. ital., XXIV, pp. 147-234, pls.
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FONTANNES, Charles Francisoue. 1887. Les Terrains Tertiaires et Quaternaires du Promontoire de la Croix-Rousse à Lyon. Arch. Mus. Hist. nat. Lyon, IV, pp. 26-44, pls. ix-xi.
GAILLARD, Claude. igoi (1goz). Le Bélier de Mendès. Bull. Soc. Anthrop. Lyon, XX, pp. 69-103 GAUDRY, Albert. I862-7. Animaux Fossiles et Géologie de l'Attique. 476 pp . Atlas of 75 pls . and map. Large 4to. Paris.

Note. -The dates of publication of the species described in this work are variously quoted; in the majority of cases the date is given as 1862 . Obviously this is not correct since the publication was spread over a period of six years. Examination of the text proved that it would be possible to ascertain the correct dates from internal evidence.

The first nine sheets have as signature a single numeral from i to 9 . Sheet io and all those which follow have for signature a number together with a date, thus io-1863. The dates are consecutive from 1863 to 1867 inclusive, and from them the following table was drawn up :

$$
\begin{aligned}
& \text { Pages i-72, publ. i862. Pages 241-323, publ. } 1865 . \\
& \text { " 73-144 " } 1863 \text {. " } 325-370 \text { " } 1866 . \\
& \text { ", 145-240 ", 1864. ", 371-end ", } 1867 .
\end{aligned}
$$

Although this does not raise any questions of priority in the case of the antelopes, published 1865 , there may be species in other groups where the question will arise.

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Note.-Entries are given for all species mentioned. Subfamilies, genera, and species dealt with in the body of the text are in small capitals. Numbers in heavy face refer to the page on which the chief reference is to be found; numbers in italics to figures in the text.

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Plate I.

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## PLATE I

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Gazella, Helicotragus.
$\square$ MUSEUM
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Plate II.


## PLATE II

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## PLATE III

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Prozoryx

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$\square$

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## PLATE VII

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Tondor Ste:evsiovic So mre
Prostrepsiceros. Microtragus.

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Palaeoryx woodzuardi
M12984


Graecoryx valenciennesi 2
M11450

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